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The response of plants to localized applications of various chemical agents

MICHAEL LEVINE

(WITH PLATES 7–9)

In a preliminary report (Levine, 1934a), it was shown that small areas of plants, painted or injected with the carcinogenic agents of animals or with some of the products of the metabolism of the tumor producing organism, *Bacterium tumefaciens*, produced slight swellings and overgrowths. Gross sections through the treated areas showed an increased thickness of the wood together with a varying degree of meristematic hyperplasia. It was further shown that there was no difference in effects produced by single or repeated paintings, nor was there any difference in the effects produced by the different concentrations of materials used in these experiments.

The following report deals with the results of a further study on the effects of coal tar, scharlach R, dibenzanthracene and ammonium hydroxide on the sunflower, *Ricinus* and tomato. Also, further data are offered on the induced bending of given parts of the stems of plants after painting with coal tar and scharlach R. In addition, the effects of applying various organic compounds bearing the -SH group and those organic substances lacking in the sulfhydryl group on localized areas of various plants are reported.

The localized application of chemicals with the purpose of producing overgrowths on plants has received considerable attention. The literature has been frequently reviewed in connection with tumor formation on plants. Here it will suffice to call attention to those papers that deal more pertinently with the problems under consideration.

Magnus (1918) studied differences in reaction between the apical and basal portions of cross sections of the carrot root grown in Petri dishes. Magnus states that the apical surfaces produced callus tissue while the basal portion produced no growth. When both surfaces of the sections were treated with a culture of *B. tumefaciens*, both produced overgrowths with the larger reaction on the apical side of the section. The amount of callus formed was greater on the treated apical surface when contrasted with the nontreated sections.

Blumenthal and Meyer (1924) studied the effects of lactic acid on sections of carrot and stems of the geranium. The tissues were scratched and a 1% lactic acid solution was applied. While most of the carrot sections became molded, these authors contend that some produced overgrowths

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which show morphological structures similar to those produced by the crown gall organism, *B. tumefaciens*.

Bittmann (1925b) studied the effects of weak solutions of lactic acid on a number of tap roots,[1] which he kept under cultural conditions. The paintings were made on alternate days. The resulting overgrowths he obtained, he attributed to the chemical stimulation of the lactic acid used.

Bittmann (1925a) also studied the effects of coal tar paintings on rabbit ears and came to the conclusion that the agent exerts its primary effects on the centrosomes. This rôle of the centrosome in malignancy in animals has recently been emphasized by Lewis and Lewis (1932). In the absence of centrosomes in the higher plants, it appears that crown gall and other reported overgrowths for these organisms cannot be referred to centrosomal behavior.

Auler (1925) investigated overgrowths on carrot sections, which he cultured in Petri dishes under aseptic conditions. He painted slices of these roots with 1/1000 of formic acid, formamid, and acetamid. Auler obtained small intumescences after 14 days, approximately the size and shape of peas, which were pale yellow in color. The formamid treated sections showed the greatest reactions, while those subjected to acetamid showed the least response. Histologically, Auler contends that the growth structure is not directly caused by the parasite, chemical or physical agent, but arises from the host tissue.

Rehwald (1927a) studied the effects of painting various concentrations of lactic acid more intensively than the former workers. He studied treated sections of roots,[2] leaves[3] and radicles,[4] and observed that repeated treatment with lactic acid tends to kill the new callus growths. I have been able to confirm these observations (Levine, 1934). Small nodules shrivel and disappear after continued painting with tar or scharlach R. Rehwald believes that the tumors formed arise from the cambium and on the bases of an histological examination of these tissues, he concluded that they are not unlike the overgrowths produced by inoculation with *B. tumefaciens*, as contended by Auler. In a later communication, Rehwald (1927b) reports further on the roots of the first mentioned series of plants and adds *Taraxacum officinale* and *Scorzonera hispanica*. He also added to his list of chemicals: 1% butter, propionacetic acid, formic acid and oleic acid copper. These were used in solution in ether or as a powder. The resulting overgrowths, Rehwald contends, are not due to the chemicals, for similar

[1] *Daucus Carota, Petroselinum, Apium graveolens, Brassica oleracea.*

[2] *Daucus Carota, Cochlearia, Armoracia, Raphanus sativus, Brassica Napus* var. *esculenta.*

[3] *B. sabauda.*

[4] *Pisum sativum, Vicia Faba* and *Citrus Aurantium.*

growths were formed without treatments. Rehwald further stresses this conclusion in another brief report (1927c) in which he states that lactic acid or any of the agents used have no specific effect on the formation of new growths on the carrot or any other roots. Injury alone is sufficient for the development of similar overgrowths.

Kendall (1930) injected a series of organic compounds[5] into growing stems of *Pisum sativum* and *Lupinus albus*. He reports that the reactions are characterized by a marked cytoplasmic enrichment of the parenchyma cells, renewed nuclear and cytoplasmic divisions which show irregularities such as polyploidy, and other aberrant chromosomal behavior. These reactions, Kendall states, were more pronounced after the treatment with acids and less marked after the injections with the enzymes. The controls, however, which were injected with distilled water, showed reactions very rarely.

Hammett, in 1928 and 1929, reported a series of studies on the rôle of organic compounds containing the -SH group on growth in animals and plants. Hammett pointed out that the roots of *Allium Cepa*, *Phaseolus vulgaris* and *Zea Mays* grown in water containing .05 mg of lead ($Pb(NO_3)_2$ for 24 hours take up the metal and deposit it in the growing center. The lead, Hammett believes, is combined in especially high concentrations with the nuclei and cell walls in this region. Cell proliferation is retarded, while cell elongation proceeds apparently unaffected. The dividing nucleus, Hammett and Justice (1929) contend, has a great avidity for lead and it is because of this that growth by cell proliferation is inhibited by the metallic ion. On the basis of microchemical tests of roots growing in solutions containing lead, Hammett believes that the lead is combined with an organic sulfhydryl compound analogous to and identical with glutathione.

Hammett contends that the root region of highest sulfhydryl concentration and mitotic activity contains a naturally occurring acid-stable, alkali-labile substance, a stimulator of root growth in length. Sulfhydryl is the essential stimulus to growth by increase in cell number. Cell size growth is not stimulated. Hammett and Reimann (1929) report that these theoretical considerations are supported by experimental data on animals. They applied thio-glucose to wounds made on the skin of normal rats. The treated skins, they contend, showed distinct acceleration of wound healing. On the basis of these observations Hammett interprets malignancy as the result of the stimulative effects of compounds bearing the -SH group. He believes that lines of cells, potentially tumor producing cells, sensitive to compounds bearing the sulfhydryl radicle, proliferate when an adequate concentration of this chemical is present.

[5] Diastase, pepsin, saliva, formic acid, lactic acid and tartaric acid.

METHODS AND MATERIALS

The present report treats of the studies of the effects of coal tar, dibenzanthracene, scharlach R, ammonium hydroxide and other chemicals mentioned on the perennials: *Salix fragilis*, *Bryophyllum calycinum*, *Opuntia keyensis*, and *Carnegiea gigantea* started in 1933 together with the annuals: sunflower, castor bean, Jimson weed, Burley tobacco and tomato, grown in 1933–4–5. These plants were all grown in a well lighted and manured open garden on the Montefiore Hospital grounds. Localized areas of the stems of thirty willow trees, 7 to 12 feet tall were painted with either 0.5%, 2% or 4% coal tar in ether or ½% or 1% scharlach R in ether three times a week. The paintings were started on August 3, 1933 and continued to December 25, 1933. The paintings were resumed on July 16, 1934 and continued to November 11, 1934. During the current year the plants were not treated but were carefully studied as to growth in general and in particular the reactions of the painted areas of the stems. The paintings of the cactus and the *Bryophyllum* plants were made with the same suspensions, started in June 3, 1933 and were continued weekly to April 13, 1934. These plants were grown in large pots in the greenhouse and were removed to the garden during the spring and summer months. The paintings were resumed on July 18, 1934 and continued to October 25, 1934.

The annuals reported before (Levine, 1934a) were studied during the growing season in the garden. They were treated with coal tar or scharlach R suspended in ether. The dibenzanthracene was applied in olive oil. In addition, a large number of each of the following plants: sunflower, *Ricinus*, *Datura*, *Nicotiana glutinosa*, *N. tabacum*, and tomato were injected with one of the following substances: .25% parathiocresol in ether, 1% thiophenol, 1% thioglycollic acid, and 1% tryptophane, each dissolved in distilled water. Weak solutions of hydrogen sulphide and ammonium hydroxide were also used. Pure, carefully prepared glutathione, cysteine, l-cystine, glutamic acid or glycine was used in powder form.

These solutions were introduced into the lumina of such plants as the *Datura* and *Ricinus*, while cavities were formed in plants with solid stems, by introducing large bore syringe needles which removed cylinders of tissue corresponding to the lumen of the needle. The powdered substances were introduced into small injuries made by ten to fifteen pricks of a sterile steel needle. Numerous controls were made by injuring only the actively growing portion of the stem. *B. tumefaciens* was introduced into a number of plants of each species. This served as a possible index of the tumor producing power of the plants used under the conditions under which the treated plants were growing. More than 600 annuals were used in 1934 in these experiments. More than 300 of the same species of annuals were

grown in 1935 to check certain phases of the results obtained in 1933 and 1934.

Young branches of three 15-year-old apple trees were amputated and the cut surfaces of the branches were painted weekly beginning July 27, 1934 to October 11, 1934 with a 1% solution of coal tar in ether or a similar solution of scharlach R in ether. These branches were carefully labelled and the callus formations were carefully noted.

The plants were fixed at supposedly critical stages in the development of the reaction tissues. These fixations were abundant and at relatively short intervals. Coal tar treated plants were fixed after each painting from the first to the twentieth. Plants fixed after prolonged treatment were found to be too woody to section for microscopic examination.

The tissues were fixed principally in Bouin solution and Flemming weaker fixative. The material was imbedded in 52°–54° paraffin and sections were made 5μ, 7.5μ and 10μ thick. Flemming's triple stain was used. Light green dissolved in oil of cloves was used after staining with an aqueous safranin. This was found to be a very desirable combination of stains for morphological studies. The nuclei take on a ruby red color with the safranin while the cytoplasm and cell walls take the light green in different intensities.

OBSERVATIONS

In a preliminary report (Levine, 1934a) on the effects of treating plants with the carcinogenic agents of animals, it was pointed out that the young injured portions of the sunflower stem painted with coal tar or scharlach R suspended in ether or pentane, in concentrations varying from ½% to 10%, produced swellings in the area of treatment. The swellings, in gross longitudinal or cross section showed increased thickness of the wood together with increased parenchymatous tissue. Stems of the *Ricinus*, when similarly treated, showed an overgrowth of tissue in the lumen of the stem. There was no macroscopic evidence of superficial overgrowths such as were described by Auler, Blumenthal and Meyer, Bittmann, Kendall and others, on taproots after painting with lactic or formic acids. There was macroscopic evidence that proliferation of tissue had occurred in excess of the numerous controls which were injured or treated with ether only. The plants inoculated with a virulent strain of *B. tumefaciens* showed the characteristic surface overgrowths now well known.

It was pointed out in that report that painting one side of the growing point of sunflower plants with ether and coal tar or scharlach R inhibited apical growth and induced open S-shaped curvatures of the stem in a large number of plants treated.

Treatment of the apical portion of sunflower stems

During the growing seasons of 1933, 1934 and 1935 more than 200 actively growing sunflower stems were treated with ether or pentane suspensions of coal tar or scharlach R. Four sets of experiments were made each year. Some plants were injured and painted at the growing region of the stem; some were just painted without injury; stems of some plants were injured and painted at the fifth and sixth leaves and some were just painted in that region. In the majority of the plants in which the growing region was painted either with scharlach R or coal tar in ether or pentane, injured or non-injured, there was a bending of the stem.

Figure 1 (pl. 7) represents two sunflower stems treated with ether and coal tar. The paintings began on June 10, 1933 and were continued to August 7, 1933. The longitudinal section in figure 1A shows the callus formed about the injured areas in the pith. The growing point has been disturbed so that there are two or three shoots arising from an arrested thickened stem. Figures 4 and 5 (pl. 7) represent longitudinal sections of two stems, one showing the cut surface. The plants were painted weekly with a 10% solution of ether and coal tar. In all, four paintings were made. The gross effects are the same as those of the injured stems. The growing region, as in the case of the injured stems, breaks up into a number of growing centers and two or more attenuated short stems are formed. There appears to be no thickening of the tissue, although it seems as if the stem at the painted areas showed a reduction in the thickness of the stem. It has already been pointed out that scharlach R suspended in ether produces similar effects.

Under certain conditions the stems bend slightly but recover and appear almost straight as in the normal. In figure 2 (pl. 7) two plants are shown, one treated with ether and coal tar (A) after injury at the growing region, the other treated with scharlach R in ether (B) below the growing region. The latter seems to have been but slightly affected. There is considerable swelling above the painted area but little bending. The coal-tar ether treated stem is dwarfed with the interfoliar spaces greatly reduced. The axillary buds develop into shoots which bear heads, producing a witches' broom effect. Pentane used as a solvent does not alter the reaction of the plant to the coal tar or scharlach R. Figure 3 represents photographs of two plants: "A" was injured and given four weekly paintings with ether. There appears to be a shortening of the interfoliar spaces, but with no bending of the stem. The photograph shown in figure 3B represents a plant that was injured and treated with coal tar dissolved in pentane. This plant was treated below the growing point over a large area

and appears to have involved the active region of the growing stem. Recovery from bending appears to have started.

During the current year these experiments were repeated and it appears that unilateral painting of the growing region of the sunflower stem induces bending. The stem is dwarfed and frequently a number of growing centers are activated, which produce stems that bear flower buds. When the treatment is applied to the stem below the growing region, there is little bending, from which the stem recovers rapidly. The injured area shows considerable swelling.

The mechanism involved in the bending of the treated stems is not clear. There appear to be a number of possibilities that may explain these phenomena. It is possible that as few as four paintings with the irritants are sufficient to inhibit the growth and division of the cells. This may be due to some osmotic change in the superficial cells as shown by Ortiz Picón (1932) and Levine and Bergmann (1936). The coat of tar or scharlach R may prevent the escape of catabolic substances while the anabolic products of the cells may stimulate unpainted normal areas. This fact is not entirely clear on the basis of sectioned material reported below. It is suggested, on the basis of the work of Went (1928) and others, that the growth hormone or auxin in the growing region of the stem is affected by the coal tar, scharlach R and probably a variety of substances still unknown, so as to interfere with the normal growth and division of the cells. The development of swellings which occurs at the injured area of the stem after painting with coal tar and scharlach R and the other chemicals referred to below seems to affect the deeper layer of cells, especially the cambium, which proliferates. This implies the movement of the growth hormone from the injured cells to the surrounding tissue. Studies on the growth hormone in the stems of the sunflower and other plants, to verify, if possible, these concepts of the mechanism of tumor formation in plants, is now in progress.

Further, it has been stressed by a number of workers that the mechanism of tumor formation in plants after inoculation with *B. tumefaciens* is not due directly to the presence of the organism itself. It is suggested here that the organism may stimulate the host cells by the liberation of growth stimulating substances. These cells are capable of perpetuating themselves for a limited number of generations while the supply of these substances lasts. It has been shown (Levine, 1936) that the *B. tumefaciens* organism when grown under cultural conditions undergoes morphological changes. These changes may be associated with physiological alteration in the parasite. Old cultures of *B. tumefaciens* are not as virulent and do not produce crown galls as readily as young cultures of the organism.

The effects of the -SH group

To study the effects of the chemicals containing the sulfhydryl group upon young plants, *Helianthus annuus*, *Ricinus communis*, *Datura stramonium* and *Nicotiana tabacum* were injected with or injured areas were powdered with glutathione, cysteine hydrochlorate, l-cystine, parathiocresol, thioglycollic acid or thiophenol. To better study the effects produced by these chemicals, some organic compounds without the sulfhydryl group were used, namely: glycine, glutamic acid and tryptophane. Coal tar in ether and dibenzanthracene in olive oil paintings were also made on a smaller number of plants, and ammonium hydroxide and hydrogen sulphide in weak dilutions were injected into another group of plants of the same species. The control plants were merely injured or inoculated in the usual manner with *B. tumefaciens*.

Glycine, glutamic acid, l-cystine, cysteine, glutathione and dibenzanthracene were applied to growing portions of young sunflower plants four to five feet tall. These substances were chemically pure and they were applied by means of a sterile wooden probe sharpened to a point, which was used to injure the plant and at the same time to introduce the agents into the tissues. Each plant was carefully labelled after the treatment. The plants were observed daily and it was noted 24 hours after treatment that slight necrosis appeared about the injuries. One week after the sunflowers were treated, it was noticed that the glutathione treated stems showed greater reactions in the form of swellings and small intumescences. Two weeks after the treatment, the glutathione treated plants showed the largest reactions of any of the treated plants and equal to the swellings produced by *B. tumefaciens*. The maximum reactions shown by the control plants were slight or moderate swellings.

The treated sunflowers were removed from the garden and sorted and measured. Longitudinal sections were made of most stems. It was noticed that the growths produced by glutathione, glutamic acid and dibenzanthracene were not much different. The *B. tumefaciens* inoculations were not as large as they had been in previous years. The comparison was made on the basis of photographs previously made.

Figures 1 to 12 (pl. 8) show a series of photographs of the sunflower stems and their longitudinal sections thirty to forty days after treatment with the various chemicals. Figures 13 and 14 represent control sunflower stems. The former shows considerable swelling in longitudinal section. Figure 2 represents a stem of the sunflower treated with glutamic acid after injury. The small intumescences are of interest and it appears as though a tumor mass is imbedded within the host tissue. Gross section (fig. 1, pl. 8) shows new wood formation and considerable parenchymatous

tissue. Microscopic examination of these stems is referred to below. It may be said, however, that the microscopic sections show considerable hyperplasia. The reactions of the sunflower stem to parathiocresol (figs. 7 and 8) are very characteristic and differ from the reactions of other plants in that thick irregular masses of tissue resembling distorted calluses are formed. The formation of wood after treatment with parathiocresol is very extensive and microtome sectioning of this tissue without the use of special methods is extremely difficult.

Growing internodes of *Ricinus* plants were injured and treated with glutathione, glycine or cysteine hydrochlorate. After three months these stems were removed and studied. The surfaces where the injuries were made were closed by scars. Longitudinal sections of these stems showed the lumina of the injured internodes filled with parenchymatous tissue in which vascular elements were found. There was no difference between the reaction of the *Ricinus* to the -SH group bearing chemicals and those that had no sulfhydryl elements in it. Figures 18, 19, 20 show the reaction of *Ricinus* to suspensions of dibenzanthracene in olive oil. While the quantity of dibenzanthracene differed, the reactions were approximately the same. Figure 18 shows a surface view of a small stem treated with .001% dibenzanthracene in olive oil. The stems shown in figures 19 and 20 received .01% dibenzanthracene. Longitudinal sections show the same type of reaction in the lumina of the stems as produced by the glutathione. I have made too few controls on the *Ricinus* but from evidence already present it appears that any internal injury to the parenchyma of these stems sets up a reaction which results in the overgrowth of the parenchyma. This new growth which fills the lumen of the injured and treated internode with the tissue, shows fibrovascular elements. This type of tissue represents the most effective reparative protection tissue the plant seems to be capable of producing.

B. tumefaciens inoculations in the *Ricinus* results in the formation of localized masses of tissue about the point of inoculation in the lumen of the stem and on the surface. Frequently the new growth fills the lumen of the internode inoculated. *Ricinus* stems were injected with 1% thiophenol and 1% thioglycollic acid. A 1% tryptophane suspension was also used. Approximately 1 cc. of the solution was injected into a young internode. It was observed that the treatment produced wilting of the stem at the injected internode. The internodal tissue became soft and collapsed due to the weight of the tissue above it. There was recovery, however; the tissue became turgid but never recovered its normal shape or position. In a number of cases the apical portion of the injected stem died, while a smaller number survived.

Few plants showed evidences of parenchymatous reaction in the lumina of the stems after treatment with the thioglycollic acid. Where there was a splitting of the tissue in the survived stems, considerable callus was formed. There was no evidence of overgrowths comparable to crown gall formation.

Ricinus stems treated with tryptophane showed scar tissue but no internal reactions. Thiophenol produces no marked reaction of the tissue in the *Ricinus* stem. Hydrogen sulphide solution in small quantities was also injected into the lumina of a number of stems. There was slight callus formation at the point of injection but no further reaction.

Stems of *Ricinus* and *Datura* plants were injected with 1% solutions of ammonium hydroxide. These injections were started in July, 1934 and were continued weekly to October of the same year. The *Ricinus* plants were injected in one of the upper internodes with 5 cc. of the solution, while the *Datura* stems were injected with 20 cc. The stems of the *Datura* plants are not septate so that the fluid accumulated in the hollow of the central stem. The stems of the *Datura* were cut longitudinally from the branch injected to the root of the main stem. A large quantity of the solution had accumulated at the base of the stem. It is reasonable to assume (Smith, 1917) that small quantities of ammonia gas were liberated in the lumen of the stem. In both species of plants scars formed about the points of injection but no hyperplasia of the tissues was found.

The *Ricinus* stems wilted at the internodes injected, resulting in death of the apical portion of the stem. A comparatively large number recovered, leaving the stem twisted at that node, an effect produced by the solutions referred to above. The lumen of the plant showed no proliferation of parenchyma. It appears as though the solution destroyed the living parenchyma which proliferates abundantly after treatment with most of the other chemicals used. Stems of *Datura* treated with glutathione, cysteine, glycine and glutamic acid produced scars, but in no case was overgrowth tissue found. Scharlach R and coal tar treated stems of Jimson weeds showed abundant surface intumescences as shown in figures 23 and 24 (pl. 8) respectively.

Continued paintings of *Ricinus*, willows and apple with coal tar show thickened calluses about the painted injured areas. Figure 21 (pl. 8) shows the effects of treating young *Ricinus* stems with coal tar in pentane for more than four months. The plants became old, flowered and produced abundance of seeds. The painted internode shows a warty mass of corky tissue. The control (fig. 22) treated with ether after injury for the same period of time shows a small internodal space but no further reaction. The lumina in both cases were filled with woody tissue characteristic of the basal internodes of the plant.

Young willow trees raised from cuttings were painted with coal tar or scharlach R weekly and thrice weekly for a period of ten months in 1933 and 1934. The calluses about the injured areas were removed four times at intervals of about two months. No overgrowths other than heavy calluses were formed. The wood which was exposed several times was completely covered. It appears that the tar treated plants healed faster and may indicate the use of coal tar as an effective agent in horticultural practice.

The midvein of the Burley variety of *N. tabacum* was injured and then subjected to powdered glycine, glutamic acid, glutathione, cysteine hydrochlorate and dibenzanthracene in olive oil. Fifty such plants were used with one to three leaves on each plant treated. Two days after treatment with cysteine, necrosis of the area treated resulted in loss of the leaf. The glutamic acid and glutathione produced necrosis to a moderate degree. The surviving leaves were harvested and examined three months after treatment. In no case was there any gross evidence of embryonic proliferation or tumor formation. Scars were formed and the treated areas healed.

The growing tips of thirty tomato plants were subjected to 1% thioglycollic acid, 1% parathiocresol, dibenzanthracene and glutathione. The glutathione treated stems showed thick scars with occasional splitting of the tissue and healing about the injuries. Puckering of the tissue about the wound appears greatest in the dibenzanthracene treated plants, three months after treatment, as shown in figure 16 (pl. 8). The injured controls show slight or no reaction except a series of concentrated needle pricks. Tomato plants growing in the same plot, inoculated with *B. tumefaciens* produced the typical crown gall as shown in figure 17 (pl. 8). The parathiocresol, thiophenol and thioglycollic acid produced necrotic areas with little or no reaction tissue.

In Jimson weeds subjected to the same treatment as the tomato, the reactions were more favorable. Thick scars were formed at the point of injection with thioglycollic acid and parathiocresol. The lumen of the stem showed proliferation of parenchymatous tissue especially about the site of injection.

The *Bryophyllum* and cactus plants reported previously showed no further reaction. No joints or proliferating branches were found in the painted portion of the plant. The actively growing stem showed larger calluses than smaller plants. The callus seemed to be thicker and formed more rapidly than those of the controls. Injected notches of *Bryophyllum* leaves that usually form crown galls after inoculation with *B. tumefaciens*, produced very slight reactions. Of the large number of leaves treated many of them were shed forty-eight hours after treatment.

Seedlings of sunflower and *Ricinus* were studied in pots in the laboratory and in the garden. The potted plants were painted with coal tar or

scharlach R. More than 118 sunflower plants with first leaves were treated with the entire range of chemicals used on the more mature plants. The potted plants reacted poorly to the treatments. Even the inoculation with a virulent strain of *B. tumefaciens* resulted in minute papillae at each point of inoculation. There were evidences of small swellings about the injuries, which consisted of a single prick of a pointed probe.

The sunflower seedlings grown in the garden grew rapidly and responded like the old plants. Sections through these seedlings 45 days after treatment with the sulfhydryl bearing chemicals showed corky swellings. The greatest reactions were obtained with parathiocresol.

In general, it may be concluded that the various chemicals showed little difference in their effects upon the plants used. Plants treated with glutathione, glutamic acid and dibenzanthracene appeared to show the greatest reactions. The compounds not bearing the -SH group showed marked reactions dependent upon the health and vigor of the plant used. This, it appears, is no argument against the importance of the -SH group in growth, but it rather points to our inadequate knowledge concerning the plants and stimuli. How coal tar, dibenzanthracene and the other carcinogenic agents produce cancer in animals is still unknown. It is clear, however, that a large number of chemicals exert a growth stimulating effect on plant cells locally treated. At present it appears that the intervention of another living organism such as the fungi or the nematodes is required to produce overgrowths in the higher plants.

The histology of chemically treated stems

An abundance of material from the different species of plants treated with various agents mentioned above, was prepared for microscopic examination. A large number of microscopic preparations were photographed at low magnification for the purpose of comparing them with the control tissues consisting of injured stems and crown galls. In plate 9 a small number of these photographs is shown. As I have pointed out in 1934, none of the chemicals used produces overgrowths comparable in size to those produced by *B. tumefaciens*. The histology of these overgrowths at comparable ages is different.

In young crown gall tissues the elements consist of disoriented parenchyma, protoxylem, and xylem elements. In the chemically treated tissues the same types of cells appear, but the disorientation and the bizarre effects appear to be less striking. While the cellular elements are necessarily the same, crown gall tissue differs from the chemically induced reaction growths in that the peripheral cells are nucleated and actively proliferating; growth is peripheral. In the chemically induced reactions

the peripheral cells, those nearest the seat of injury frequently hypertrophied, are large and mature and generally show no nuclei. Nuclear and cell divisions occur in cells surrounding the peripheral layer of cells. Parenchymatous tissue with fibrovascular elements occur in both types of tissue. However, there are variations of this state, as mentioned below. Cytological studies of tissues twenty to thirty days after treatment show large cells with small nuclei. These appear to be mature cells at this time and do not present embryonic appearances characteristic of neoplastic tissue. Few division stages have been observed. In preparations made a week after treatment, proliferating cells have been observed. The cell and nuclear divisions are normal and the chromosome groups are relatively clear. There is no evidence of polyploidy in these preparations although no special study of chromosomes has been made. Binucleate cells are of frequent occurrence.

It has been pointed out above that crown gall tissue presents certain characteristics that differentiate it from the chemical reaction tissue. Figure 4 (pl. 9) represents a photomicrograph of a section of a crown gall on the sunflower 49 days after the stem tissue was inoculated with *B. tumefaciens*. The active cells occupy a broad peripheral margin of the gall. The cells are small, embryonic in appearance, and are typical of crown gall tissue (Levine, 1931). The terminal cells have formed a corky covering over the surface of the gall. Hypertrophied, large, parenchymatous cells also form part of this tissue.

Scar tissue formed after injury, in a control plant, is shown in figure 1 (pl. 9). This specimen was taken from a sunflower stem five weeks after needle wounds were made in the young terminal portion of the stem. The surface of the section shows corky cells. The tissue lying on both sides of the deeply stained area of injury, shows layers of hypertrophied cells; few nuclei are present. There is evidence that in the development of the new tissue, the cells were active, but at this period the cells are mature or old. A tendency to form a corky covering over the injured area is obvious.

Sections made of control sunflower stems, 5, 21 and 27 days after injury show in the first case, considerable proliferation of the meristematic tissue around the fibrovascular bundles. The cells are small with comparatively large nuclei. The cells about the injury appear hypertrophied. The stimulation of the meristematic cells in the control specimens results in extensive proliferation of this tissue; the cells mature early and form considerable wood which increases the thickness of the stem above the normal. This is evident in specimens 27 days after injury. Space will not permit the publication of these photographs. Histologically, these preparations resemble closely the chemically treated stems.

Coal tar suspended in ether when applied to injuries in stems of the tobacco (*N. tabacum*) produces small scars about the surface injury and woody tissue is formed about the traumatized tissue in the pith. The thickness of the wood is increased as shown in figure 15 (pl. 8). Fixation of the scar tissue has in several cases revealed the presence of internally formed embryonic rootlike structures as shown in figure 2 (pl. 9). The embryonic reaction tissue is present but surrounded by a mass of parenchymatous cells; one observes small thick-walled cells from which the embryonic rootlike structures make their appearance. These bodies resemble the rootlike structures observed in crown gall on *Opuntia keyensis* (Levine, 1934 b). The presence of these embryonic rootlike structures does not imply that coal tar is specific for these *Anlagen*. The cellular reactions in the tobacco are abundant and capable of differentiating into these embryonic growths. No embryonic leaves were observed. The evidence from the present studies and those on crown gall previously reported, seems to indicate that the tobacco is capable of responding in this manner. One may conclude that the type of response is a function of the host rather than the stimulus.

The selected area shown in figure 2 represents only one of many of these regions in the treated stem, in which the embryonic structures could be definitely identified as the longitudinal sections of roots. Some of the structures were further advanced than the one shown in this figure. Sunflower stems treated with coal tar for five weeks during which time nineteen paintings were applied to a small injured area of the stem, showed considerable swelling. On sectioning the stem through the injured area one finds a mass of necrotized cells. Radiating from it are slightly hypertrophied cells with smaller embryonic types of cells on the surface of the mass of tissue, surrounding the area of injury. The whole is buried between strands of fibrovascular bundles. Meristematic tissue is involved in deep injuries. Protoxylem cells are found and the xylem appears later. These injuries present distinct pathological structures which are not readily separable from the crown gall tissue. The extent of the reaction varies in the different species and in the individuals in a species. These sections differ little from those of stems treated with dibenzanthracene.

Specimens of sunflower stems painted once with coal tar in ether and fixed twenty–two days after the treatment showed a prolonged duration of the proliferation period, thus forming a great mass of embryonic cells. This suggests the possibility that the repeated paintings induce early maturity of the treated tissues, due possibly to interference with the metabolism of the newly formed cells.

Figure 3 (pl. 9) represents a section of a sunflower stem treated with coal tar in ether once weekly for ten weeks. The reaction tissue is clearly

shown in the upper part of the photograph, while the normal cortical tissue is seen in the lower part. Note the binucleate cells in this tissue. Histologically this tissue is quite comparable to crown gall (see fig. 4, pl. 9). The principal difference between these tissues appears to be one of quantity. In both reactions, crown gall and chemical stimulation, there are cellular proliferations at first and then differentiation; the types of cells involved are the same. The chemically stimulated tissue has a short embryonic life, while crown gall proceeds further in piling up a greater mass of embryonic tissue before differentiation and old age set in. In animal and human cancer, cell proliferation is generally considered limitless. While the animal and human pathologist can, in most cases, recognize malignity and overgrowths on the basis of a microscopical examination of the tissue, in plants the absence of an overgrowth makes the diagnosis of a tumor, such as crown gall, difficult.

Sunflower stems treated after injury with compounds bearing the sulfhydryl group show microscopically a layer of large cells about the traumatized tissue, surrounded by a layer of small, active, embryonic cells. In this, the reaction is identical with the nonsulfhydryl bearing compounds used in these experiments. Figure 5 (pl. 9) represents a section of a sunflower stem ten days after injury and a single application of tryptophane. This section was made through the reaction tissue. The upper surface of the figure represents the traumatized cells, while the active cells occupy the central portion.

Stems treated with thiophenol, parathiocresol, cystine, cysteine, glutamic acid and glycine give similar reactions. Preparations of sunflower stems made after treatments with these chemicals are so much alike that one cannot be separated from the other.

In glutathione preparations such as the one shown in figure 6 (pl. 9), the overgrowth consists of stimulated meristematic tissue coupled with hypertrophy. The upper margin of the figure represents the injured cells. Below this layer, as in all the chemically treated tissues, one finds the mature parenchymatous cells and below this, the layer of active cells. In this specimen, the active cells appeared larger than usual.

According to Eckert, Cooper and Seelig (1935), scharlach R is not carcinogenic for young white rats. In these plant studies, the scharlach R treated sunflowers very frequently elicited greater swellings than any of the chemicals used.

Figure 7 (pl. 9) represents a section of a tomato stem painted four times from the 12th of July to the 19th, with scharlach R suspended in ether. The necrotized tissue runs through the middle of the figure. Hypertrophied and hyperplastic cells are seen on both sides of this area.

Binucleate cells are common, although the chromosome number was not definitely established. The chromosome masses in these cells appeared of uniform size. Here again, as in figure 3, we have all the characteristics of young, undifferentiated crown gall tissue lacking, however, in the proliferating power and quantity of tissue to form an overgrowth. None of the chemically treated stems produced overgrowths comparable with the crown gall or other neoplastic tissues in plants.

SUMMARY AND CONCLUSIONS

1. A further study of the effects of treating plants with various chemical substances is reported.

2. Painting the apical part of the stem of the sunflower each week with a solution of coal tar in ether or pentane or scharlach R in ether, produces bending of the stem. The plant remains dwarfed and the growing point often gives rise to several small apical branches, producing a witches' broom effect.

3. Stems of sunflower, *Ricinus*, *Datura*, tomato, tobacco and leaves of tobacco and *Bryophyllum* treated with substances such as glycine, glutamic acid, l-cystine, cysteine hydrochlorate, glutathione, thiophenol, parathiocresol, thioglycollic acid, produce scars and swellings of the treated area, which had been previously injured. The swellings are larger than those induced in control specimens by merely injuring them. There is no specific difference in the reactions on plants produced by the compounds bearing the -SH group and those without it. Glutathione and glutamic acid treated stems consistently showed greater reaction.

4. An histological study of the swellings of these stems produced by injury and chemical treatment shows that the reaction tissue is limited in quantity and its location is generally peripheral to the injury. In the injured stems of the controls, the type of reaction is the same but quantitatively smaller; while in the crown gall the actively growing tissue is abundant and is located on the periphery of the gall. The same types of tissues are found in all three cases but the difference lies in the rate of division, differentiation and ageing. Comparatively, crown gall cells divide rapidly, and differentiate and age slowly. Cells of reaction tissue induced by injuries with chemical treatments divide slowly but differentiate and age rapidly. When these tissues are contrasted with the behavior of cancer we find the latter divides rapidly and indefinitely, differentiates slowly and imperfectly and is frequently supervened by necrosis.

5. Chemically induced reaction tissues, when compared with other hyperplasias of plants and animals, are the smallest and simplest types of overgrowths which never reach the malignant stage. In crown gall, tissue

proliferation is more abundant than that induced by injury and chemical stimulation, but limited when compared with neoplastic disease of animals and man. It appears that while the chemical stimulants now known induce greater reactions than the controls, the plant's protective mechanism seems to inhibit continued responses to continued applications of the same stimulus. The isolation of the chemical agent that is responsible for growth stimulation and improved methods of applying this stimulus may eventually overcome this inhibition so that the artificial application of this substance may result in overgrowths in plants, similar to crown gall, club root, potato wart, cedar apple, and galls produced by insects or nematode infestations. The nature of the response seems to be a function of the host rather than of the stimulus.

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Explanation of plate 7

Fig. 1. A, B. Sunflower stems, growing region painted weekly, after injury, with coal tar suspended in ether. Begun 6.10.33 and terminated 8.7.33. ×⅓.

Fig. 2. A. Sunflower stem, noninjured, painted weekly from 6.10.33 to 7.6.33. B. Sunflower stem painted after injury with scharlach R and ether. Treatment below growing region of stem. ×⅓.

Fig. 3. A. Sunflower stem, control, injured and painted weekly in growing region with ether from 6.24.33 to 8.7.33. ×⅓. B. Sunflower stem injured and painted below growing region with coal tar suspended in pentane. ×⅓.

Fig. 4. Longitudinal section of uninjured stem painted with coal tar in ether. Compare with figure 1. ×⅓.

Fig. 5. Sunflower stem painted once weekly for one month with coal tar in ether, no injury. ×⅓.

LEVINE: CHEMICAL AGENTS

Explanation of plate 8

Photographs on this plate were reduced one quarter normal size.

Sunflower stems

1. Treated with glutamic acid. 7.17.34. Removed and photographed 8.10.34. Longitudinal section.
2. Note intumescences after treatment with glutamic acid; photographed 8.27.34.
3. New growth emerging from injured area after treatment with glycine; photographed 8.27.34.
4. Longitudinal section of stem after similar treatment.
5. Swellings about injury after treatment with l-cystine, 7.17.34; photographed 8.9.34.
6. Longitudinal section of stem; overgrowths about injured area.
7. Injured and treated with parathiocresol; photographed one month later.
8. As in 7, showing irregular nodular masses about area of treatment.
9. Stem treated with glutathione on 7.17.34; photographed 8.10.34.
10. Longitudinal section of stem after similar treatment.
11. Stem after injured area was treated with cysteine hydrochlorate on 7.17.34; photographed 8.27.34.
12. Longitudinal section of another stem, similarly treated; photographed 8.27.34.
13. Stem of control sunflower injured; showing swellings about injuries.
14. Injured stem; control, slight swelling, marked necrosis.
15. Longitudinal section of *N. tabacum* after 18 paintings with coal tar suspended in ether. Paintings began 7.12.33. Last painting 9.2.33; photographed 10.12.33.

Tomato stems

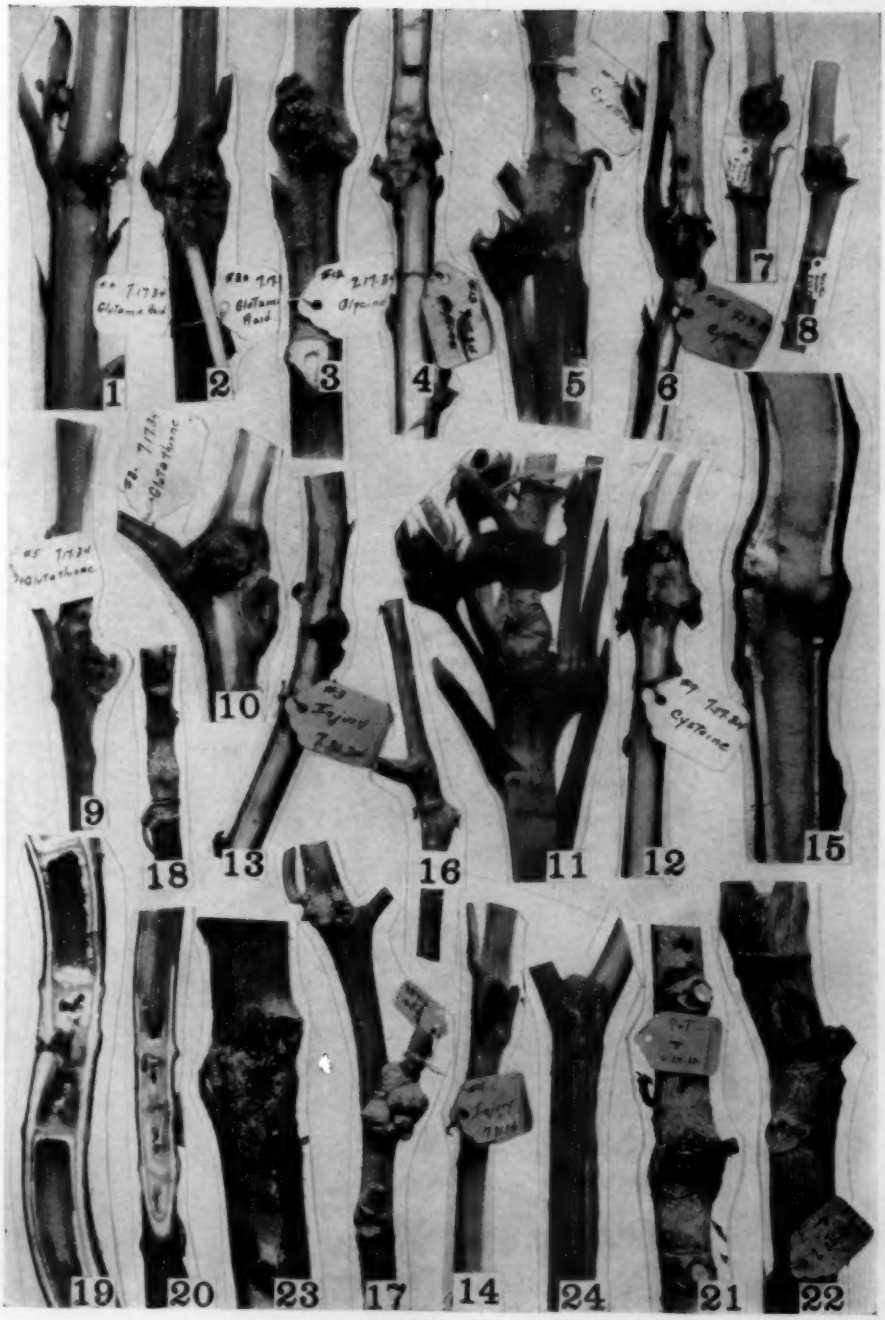
16. Treated with 10% dibenzanthracene in olive oil, after 2 months.
17. Two months after inoculation with a virulent strain of *B. tumefaciens*.

Ricinus communis stems

18. Two months after treatment with .001% dibenzanthracene in olive oil.
19. Longitudinal section of stem after treatment with .01% dibenzanthracene.
20. After treatment with .01% dibenzanthracene.
21. Injured and treated with coal tar suspended in pentane. 6.24.33; photographed 11.4.33.
22. Control; injured and treated with ether only; photographed 17 weeks later.

Datura stramonium stems

23. After 18 paintings with scharlach R in ether; 7.10.33 to 9.2.33; photographed 10.1.33.
24. After injection with 4% coal tar in ether; 8.2.33; photographed 10.1.33.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Explanation of plate 9

Figures on this plate were made with the Carl Zeiss 35 cm. photomicrocamera. The combination of lenses used is as follows: Obj. 10. Oc. 3. Bellows 75 cm. Estimated magnification ×90. K_2 filter was used with W.W. panchromatic M plates.

Fig. 1. Sunflower stem, control, five weeks after injury.

Fig. 2. From scar and pith of tobacco stem painted with coal tar in ether 17 times. (Begun 7.12.33; last painting 9.2.33). Note embryonic rootlike structure imbedded in parenchymatous tissue.

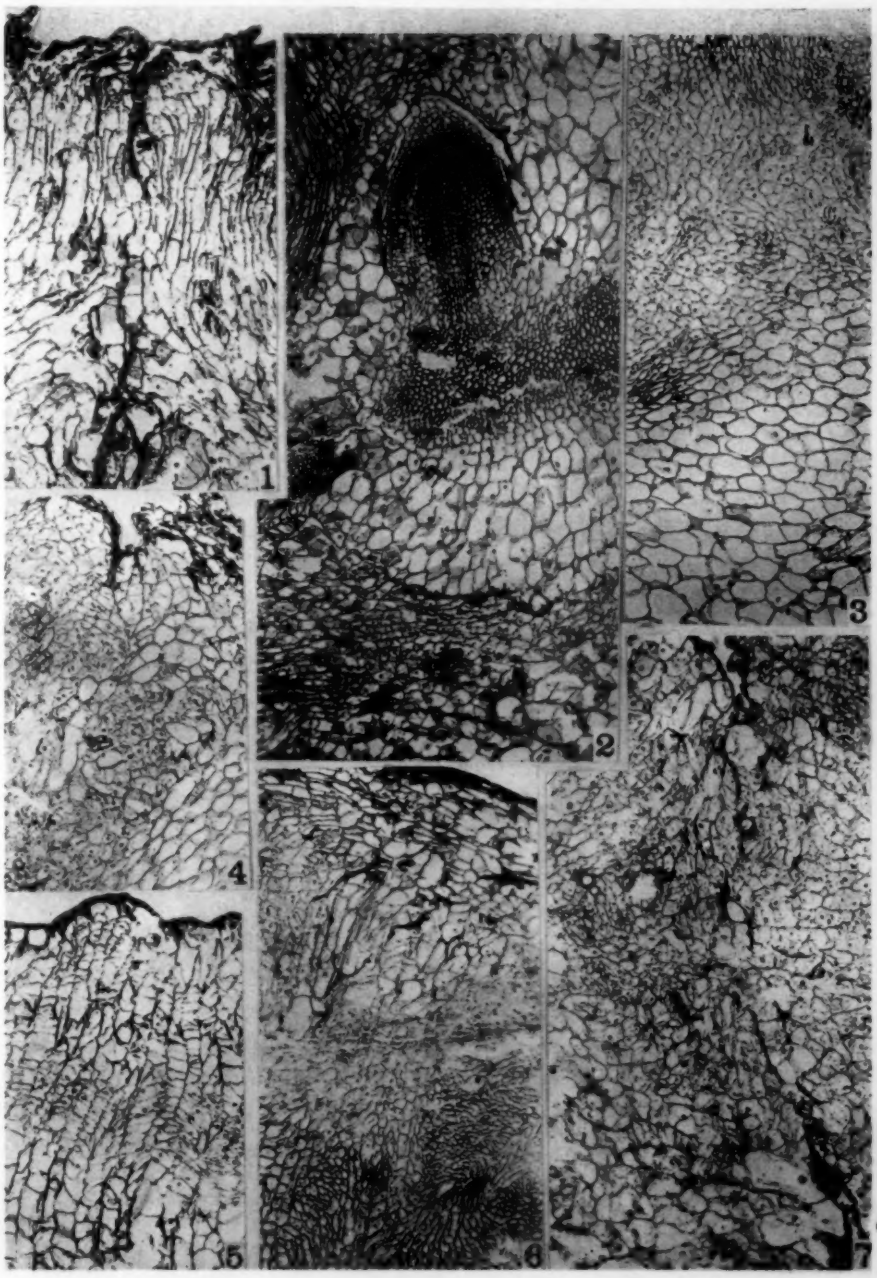
Fig. 3. Sunflower stem near growing point injured and painted with coal tar suspended in ether (10 paintings; 6.17.33 to 8.23.33).

Fig. 4. Sunflower stem crown gall tissue 49 days after inoculation with a virulent strain of *B. tumefaciens*.

Fig. 5. Sunflower stem 10 days after injury and treatment with tryptophane.

Fig. 6. Sunflower stem 40 days after injury and treatment with glutathione.

Fig. 7. Tomato stem painted with scharlach R in ether, four times; 7.12.33 to 7.19.33.



LEVINE: CHEMICAL AGENTS

A new Sedum from Texas

EDWARD J. ALEXANDER

For the past three years the writer has had under observation at the New York Botanical Garden plants of a *Sedum* received from Mr. A. R. Davis of Marathon, Texas, communicated through Mr. Leon Croizat.

At first sight the plant did not appear like any species ever known to us, but is seemed advisable to grow it through several flowering seasons for checking. After three seasons there seems no further doubt as to its being an undescribed species, not closely related to any known in North America. The writer therefore proposes the name

Sedum Robertsianum sp. nov. Sect. Seda genuina (Eusedum) § Diversifolia· Planta caespitosa, ramis a basi numerosis decumbentibus 8–12 cm. longis anno secondo florentibus, in parte erecta bifurcata, interdum simplici; foliis alternis glabris turgidis ovoideis, 3–4 mm. diam., 5–8 mm. longis, apiculatis; floribus solitariis supraxillaribus in parte caulis erecta 5-(rarissime 4-) meris; sepalis 2 externis quam interioribus multo majoribus, quam petalis dimidio brevioribus; petalis 4 mm. longis lanceolatis flavis, secus lineam mediam usque ultra medium canaliculatis, ultra medium foveolatis; staminibus petalis oppositis primum reflexis et in canaliculis accumbentibus, demum erectis.

Type collected by A. R. Davis in Brewster Co., Texas, growing at about 4000 feet elevation on a mountain top in shallow calcareous soil. Description made from plants growing under cultivation at the New York Botanical Garden.

The species is named after Mrs. Kate Roberts, upon whose ranch the original plants were collected. Mr. Davis writes: "The plants are found in lime formation nearly always on top of the highest point of the mountain and in very shallow soil. It is never found low down or in the valley so far as I have been able to determine. It is native to Brewster Co., Texas, and distributed pretty well all over the county."

An erect-sprawling succulent, perennating by short winter shoots which elongate into flowering stems the following year. The leaves on the winter shoots are somewhat imbricated, few in number compared with related species, narrowly ovate, obtusish. The fleshy stems are strongly red-streaked and spotted. The leaves at first are flattened on the ventral side especially towards the tip, the leaf becoming very turgid when fully mature, and broadly elliptical in cross section, except for keels on the sides near the tip. The mature leaves are ovoid, glabrous, yellow-green heavily spotted with red when grown in sun, 5–8 mm. long, and 3–4 mm. in diameter at the point of greatest thickness, the tip obtusely apiculate, slightly upturned. Those on the inflorescence are somewhat smaller, more pointed and less

rotund. The leaves, even under a hand lens, appear minutely papillose, but under the microscope it will be seen that this is an optical illusion caused by the reflections from the inner facets of windowed cells of red, green, and transparent color. The inflorescence is two-branched or sometimes simple, apparently through suppression of other branches, as indicated by short side branches on some inflorescences near the base, which bear one leaf and a single flower. The bright yellow flowers are about 1 cm. across,

Fig. 1. *Sedum Robertsianum* Alexander, ⅔ natural size.

equilaterally arranged, and are, even to the lowest, supra-axillary, each very short-stalked or sessile, and having normally a much smaller leaf-like bract not immediately subtending it. On normally developed inflorescences, each branch bears six to twelve flowers. The two outer sepals are much larger than the three inner (in four-parted flowers two large and two small), all lanceolate, the larger half the length of the petals, the smaller half that size. The petals are narrowly lanceolate, about 4 mm. long, greenish at the base, bright yellow above, channelled on the upper surface, the channel deepening into an elliptical pit at a point about two-thirds way up, the pit protruding as a shallow knob on the under surface. When the flower opens, the five stamens alternate with the petals are erect, the five opposite the petals are reflexed, the anthers resting in the pits, and after

anthesis of the calycular series, the corollar series becomes erect and sheds its pollen, after which all ten reflex. The four or five carpels are erect at anthesis, afterwards slowly spreading. The body is oblong-conical, the tips subulate, about one-fourth the length of the body. The mature fruit has not yet been seen.

This species is unique among true sedums in its inflorescence and leaves. In view of its known area of occurrence it should be looked for in the neighboring section of Mexico.

In common with certain others of the genus, the leaves, which are easily detached, will, if left undisturbed, sprout from the severed base within a few days, thus forming an easy method of propagation.

NEW YORK BOTANICAL GARDEN

A method of cultivating myxomycete plasmodia

W. G. Camp

(with five figures)

Methods of cultivating slime mold plasmodia for research and instructional purposes have long been a subject of major interest in research laboratories and in schools. A review of the literature on the use of nutrient substrata for such cultures has been given by Howard (1931) and he has reported the successful culturing of plasmodia on oat agar. The writer has employed Howard's method and has found it successful, but after some experimentation has devised another method of growing plasmodia by feeding them rolled oats without using an agar base. The advantages of the method here described obtain from the facts that relatively enormous quantities of plasmodia can be produced in a single culture with little labor and care, the plasmodia can be easily separated from the material of the substratum, and given cultures can be maintained for a relatively long time and fed periodically.

The material used in this work was obtained as a deep yellow sclerotium formed by the desiccation of a lemon yellow plasmodium in the laboratory. Cultures were first grown from fragments of the sclerotium in petri dishes on oat agar. In the course of time some of the cultures formed sporangia and the form was identified as *Physarum polycephalum* Schw.

The method of culturing which has been developed is as follows: the upper surface of a Petri dish is covered with gauze or filter paper and the edges are folded under the rim of the dish. This is placed, inner face down, in a battery jar or similar vessel containing water to a depth of about one centimeter and which can be covered with a glass plate. Living plasmodial or sclerotial fragments are placed on the gauze or filter paper where capillary water affords moisture for the substratum. Water in the battery jar must not be of such depth that the gauze or paper is flooded. The plasmodia so far observed appear to be very markedly aerobic, and a substratum flooded with water is not conducive to good growth and activity. When a piece of living plasmodium is placed on the moist surface, it will very soon begin to creep and spread over this surface (fig. 1) and if a sclerotium is placed there, an active plasmodium emerges in a few hours (fig. 4). In either case, after the plasmodium has spread over a portion of the moist surface, feeding may begin. This is provided for by sprinkling a small amount of pulverized rolled oats directly on the plasmodium (fig. 2). The plasmodium creeps up around the oat particles and appears to feed by ingesting and surrounding them directly (fig. 3). When starting a culture care must be exercised against using an excessive quantity of crushed

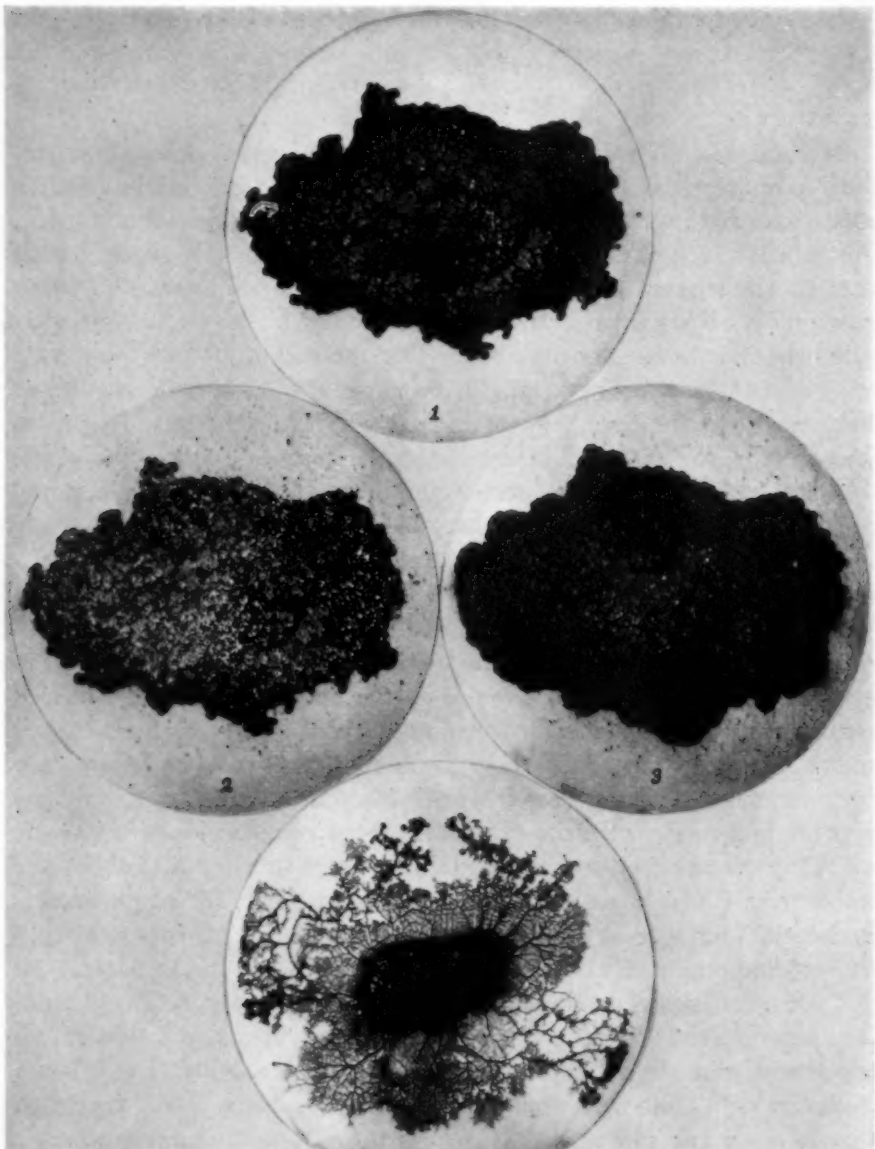


Fig. 1. Plasmodium spread over moist substratum.

Fig. 2. The same plasmodium as in figure 1 with pulverized rolled oats sprinkled over its surface.

Fig. 3. The same plasmodium as above thirty minutes later. The plasmodium has surrounded most of the oat particles.

Fig. 4. Plasmodium which emerged from a sclerotium (dark mass in the center of the photograph).

oats, and a little experience at this stage of culturing soon enables one to determine the quantity that should be used. An excessive quantity placed over the plasmodium or on areas of the moist substratum not occupied by the plasmodium tends to promote bacterial and fungus growth, and the culture may suffer from the growth of these other organisms. Following the initial feeding stage the plasmodium grows and spreads over a wider and wider area and finally is distributed over the whole moist surface. In the early stages of culturing, feeding is repeated as often as the plasmodium completely surrounds all of the oat particles from the previous feeding. Finally a very luxuriant plasmodium covers the whole surface of the substratum and at each subsequent feeding crushed oats may be sprinkled on the plasmodium until there is a more or less continuous covering layer. Plasmodial strands creep up between the particles of oats, and within the space of a few hours appear to have all of the particles completely surrounded. After the plasmodium attains considerable size, noticeable growth of fungi and bacteria in the nutrient substratum seldom occurs.

As the plasmodium grows, it creeps down the gauze or paper, which extends into the water, until the water level is reached and then across the surface of the water and up and over the inner surface of the culture vessel (fig. 5). To facilitate rapid spread of a plasmodium from the substratum on which it is growing to the wall of the culture vessel, the petri dish supporting the substratum is placed flush against the wall of the vessel. This direct contact obviates the necessity of the plasmodium creeping over the surface of the water, and almost invariably plasmodia tend to follow the bridge thus provided rather than creep over the water surface. Where the plasmodium comes in contact with water, it produces a copious amount of slime which has the appearance and consistency of egg white, but on dry surfaces or surfaces which are only slightly moist, a comparatively small amount of slime is produced.

When a culture is once well established, by following the method described, it requires on the average, no more than a few minutes of attention each day to gather the plasmodium from the walls of the culture vessel, remove the Petri dish so as to be able to wash the vessel, feed that portion of the plasmodium which remains on the supporting substratum and set the culture up for another daily period of growth and expansion. The writer has maintained cultures set up in this way for periods longer than two months, and from each culture has gathered relatively enormous quantities of protoplasm freed of all of the material of the substratum. The living plasmodia may be gathered from the walls of the vessels in various ways. At times plasmodia form dense compact masses covering an area ranging from a few to several square centimeters, which masses

may become several millimeters thick. Accumulations of this type may be harvested by removal with a broad flat instrument such as a section lifter or spatula. Again the plasmodia may distribute themselves as thin reticula over the surface of the glass. A recticulum may be gathered by first removing the petri dish with its covering of nutrient substratum, then washing the reticulum from the wall of the vessel with a small stream of water, and finally lifting the clumps and strands of protoplasm from the water or separating them from the water by filtering. A third method of

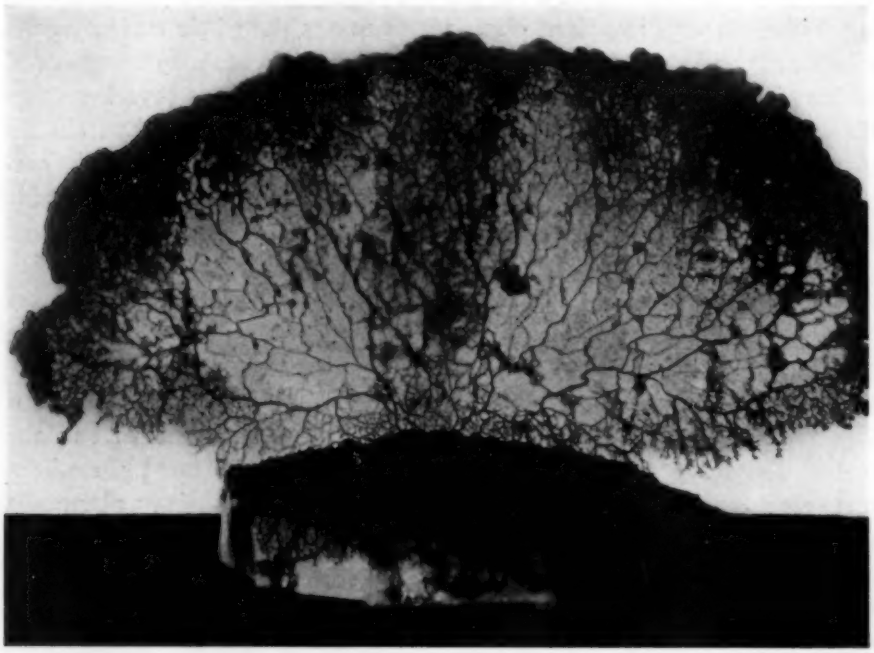


Fig. 5. Plasmodium which has spread from the substratum to the inner surface of the culture vessel.

gathering plasmodia which is very easy and labor saving if one wishes to produce sclerotia, is to line the inner sides of the culture vessels with sheets of paper of appropriate size. Almost any kind of paper is satisfactory but a smooth paper is preferred as compared to paper with a rough or corrugated surface. Plasmodia creep on to and over the paper and at an appropriate time the sheets themselves are removed from the culture vessels with the protoplasmic recticula spread over and clinging to their surfaces.

The habit of some of the Myxomycetes of forming sclerotia and the general conditions under which sclerotial formation takes place have long

been known. This habit can be utilized advantageously in preserving viable material and obviates the necessity of maintaining living cultures of plasmodia for future use. The writer obtains sclerotial formation by slow desiccation of plasmodia on paper. This desiccation is accomplished at room temperature by placing plasmodia on sheets of paper under bell jars and providing a very small opening so that slow exchange of gases can take place between the atmosphere of the bell jar and the external atmosphere. The optimum conditions for sclerotization have not been determined but if desiccation is too rapid, the plasmodia form horny nonviable masses. It is effective to extend the period of desiccation over a twenty-four hour period. During sclerotization the protoplasm of a plasmodium forms one or more compact masses which may vary in thickness up to more than five millimeters but with continued desiccation this thickness usually decreases to less than two millimeters. The fully formed sclerotia whose color may vary from brilliant lemon yellow to light brown may be removed from the paper on which they are formed and preserved at ordinary temperatures. They have remained viable after exposure to the temperature of liquid air for ten minutes and after exposure to a temperature of 52°C. for two weeks. Furthermore, fragmentation of sclerotia does not destroy their viability. A finely ground mass obtained by pulverizing a sclerotium produces an active plasmodium at room temperature when afforded the proper conditions of moisture.

The utility of culturing myxomycete plasmodia by such a method as has been described is at once suggested. Unlimited quantities of naked protoplasm can be obtained for use in chemical and physical research studies. Comparatively few such studies on the plasmodia of slime molds have been made, which fact has undoubtedly been due to the difficulty of obtaining sufficient quantities of material. It is worth noting that in the chemical studies of Walter (1921), Lepeschkin (1923), Kiesel (1925, 1927) and Iwanoff (1925), the materials used were collected from substrata upon which slime molds naturally occur. The difficulties and limitations of collecting plasmodia from their natural substrata for use in such studies are obvious. Furthermore, this method of culturing is adapted to experiments such as those which demonstrate the relationship of hormones, vitamins and auxins as well as the better known constituents of dietary substances to growth and development. Such experiments should be more fundamentally significant than similar experiments with the embryonic and later developmental stages in the higher plants and animals on the one hand and with tissue cultures on the other hand. A plasmodium is relatively free of the complexities of organismal differentiation characteristic of the higher plants and animals, yet it feeds and grows and reaches

reproductive maturity. In this latter respect it is fundamentally different from ordinary cultures of isolated tissues such as those of Carrel (1912) and Ebeling (1921) for animal tissues, and those of Robbins (1922) and White (1934) for plant roots and stems.

The procedures here described have been applied extensively to only one species of slime mold, namely, *Physarum polycephalum*. Experiments with other forms are being made and more exact quantitative data as to nutrient materials, temperature, moisture, light and other relations will be obtained.

The writer is indebted to Dr. R. A. Harper and to Dr. J. S. Karling for assistance in the preparation of the manuscript.

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A revision of the genus Axinaea (Melastomaceae)[1]

DONALD S. EVES

The genus *Axinaea* was proposed and first described by Ruiz and Pavon (Prodr. **68.** 1794). This description was based upon *A. lanceolata* Ruiz & Pav. and *A purpurea* Ruiz & Pav. *A. purpurea*, however, was transferred at a later date to the genus *Meriania* as *M. purpurea* (Ruiz & Pav.) Sw. (Fl. Ind. Occ. **2:** 829). DeCandolle (Prodr. III: 102. 1828) described the genus *Chastenaea*, which he considered to be closely related to *Axinaea* and distinguished from it by a truncate and entire calyx-limb, one-pored anthers, and rotund connectives. Naudin (Ann. Sci. Nat. III. **18:** 120. 1852) regarded *Axinaea* as a doubtful genus. He transferred some of its species to *Chastenaea*, and questioned the remaining ones as being dubiously placed. These questionable species were later transferred to other genera by other workers. Triana (Trans. Linn. Soc. Bot. **28:** 69. 1871) re-introduced the name *Axinaea* to take the place of *Chastenaea*, considering it to be the valid one because of priority in use. *Axinaea* species have sometimes been confused with *Meriania* species, and transfers have been made from one genus to the other in both directions. In this paper twenty-two species are included in the genus *Axinaea*, one of which is new.

The taxonomic position of *Axinaea* is in the tribe Merianiae of the family Melastomaceae. The genus is most closely related to *Meriania*, from which it differs principally in the character of the anther-connectives: in *Axinaea* these have a thick and often inflated appendage in the rear; whereas in *Meriania* they have a blunt or pointed projecting spur at the base in the rear, and often a second spur ascending parallel to the anther-sacs and situated above the first spur.

This study, conducted at the Britton Herbarium, was undertaken at the suggestion of Dr. H. A. Gleason, to whom I am especially indebted for guidance and assistance during the course of this undertaking. I also wish to thank the following institutions for their courtesy in lending herbarium specimens: The Conservatoire Botanique, Geneva (G), the Botanisches Museum, Berlin (B), the Royal Botanical Gardens, Kew (K), the Field Museum, Chicago (F), and the New York Botanical Garden, New York (Y). The initials in parentheses are those used in the taxonomic treatment below to designate the location of cited specimens in the various herbaria.

DISCRIPTION OF THE GENUS

AXINAEA Ruiz & Pav. Prodr. **68.** 1794.

[1] Submitted in partial fulfillment of the requirements for the degree of Master of Arts in the Faculty of Pure Science. Columbia University.

Chastenaea DC. Prodr. III. 102. 1828.

Flowers 5-merous (4-merous in *A. crassinoda* Triana); hypanthium hemispheric, campanulate, or cyathiform, glabrous or furfuraceous; calyx-limb truncate or shortly and broadly lobed; petals commonly obovate, occasionally oblong or suborbicular, rounded, retuse, or apiculate, usually slightly asymmetrical, imbricate in the campanulate corolla; stamens 10, equal or subequal; filaments glabrous, flattened, broad; anther-sacs straight or slightly arcuate, linear-subulate, minutely 1-pored at the apex; connectives vesiculate, inflated and appendiculate in the rear, sometimes radially flattened; style filiform or robust, erect or arcuately declined, sometimes abruptly curved at the top; stigma truncate or attenuate; ovary free, glabrous, 5-celled, subcylindrical, ovoid, or obovoid, 5-lobed at the apex; fruit a capsule included in the hypanthium or with the apex exserted, 5-valved; seeds many, oblong-pyramidal.

Shrubs and trees; branchlets terete or tetragonal, sometimes greatly swollen at the nodes or with prominent stipule-scars, glabrous or pubescent; leaves opposite, ovate, elliptical, or oblong, acute, obtuse, or apiculate at the apex, cordate, auriculate, or subrounded to attenuate at the base, the basal margins often shortly revolute-decurrent, petioled (scarcely so or not at all in *A. sessilifolia* Triana), entire or sinuately toothed, 5–9-nerved, sometimes plinerved, glabrous or pubescent beneath, coriaceous (scarcely so or even membranaceous in a few species); petiole slender or stout, glabrous or pubescent, sometimes dilated at the apex with the lower leaf-margins confluent over it to form a transverse tubercled scutum; stipules deciduous (persistent in a few species); flowers large, white, rose, red, or purple, in broad terminal or axillary panicles.—Twenty-one species of tropical Andean South America from Venezuela to Bolivia, and one species from Costa Rica.

The type species is *A. lanceolata* Ruiz & Pav.

KEY TO THE SPECIES

a. Stipules persistent, or stipule-scars prominent as thickened rings b.
  b. Leaf-base cordate c.
    c. Leaves sessile or very nearly so. 1. *A. sessilifolia*
    c. Leaves conspicuously petioled. 2. *A. crassinoda*
  b. Leaf-base not cordate d.
    d. Branchlets conspicuously tetragonal, greatly swollen at the nodes. 16. *A. robusta*
    d. Branchlets obscurely tegragonal, scarcely swollen at the nodes e.
      e. Petiolar-scutum present; leaves 5–7-nerved. 17. *A. costaricensis*
      e. Petiolar-scutum absent; leaves 5-pli-nerved. 10. *A. dependens*
a. Stipules deciduous, stipule-scars not prominent as thickened rings f.
  f. Leaves densely ferruginous-tomentose beneath g.
    g. Tomentum of leaves furfuraceous or shortly stellate; leaf-base usually auriculate, with the auricles sometimes reflexed h.
      h. Branchlets obscurely tetragonal or terete. 3. *A. glandulosa*
      h. Branchlets acutely tetragonal. 4. *A. Weberbaueri*
    g. Tomentum of leaves elongate and plumose; leaf-base acute i.
      i. Petals less than 15 mm. long; hypanthium 7 mm. wide; petiolar-scutum present but sometimes much reduced. 5. *A. tomentosa*

i. Petals more than 20 mm. long; hypanthium 12 mm. wide; petiolar-scutum absent. 6. *A. sclerophylla*

f. Leaves glabrous or merely somewhat furfuraceous beneath (whitish-arachnoid in *A. lepidota*) j.

j. Branchlets and lower leaf-surfaces whitish-arachnoid, especially when young; upper leaf-surfaces nigrescent when dry; leaves 3–5 cm. long, 3–5-pli-nerved. 22. *A. lepidota*

j. Branchlets and lower leaf-surfaces never whitish-arachnoid; leaves usually more than 5 cm. long k.

k. Leaf-base cordate or auriculate, with the lobes sometimes small and reflexed l.

l. Leaf-margins entire. 14. *A. Lehmannii*

l. Leaf-margins toothed m.

m. Petiolar-scutum absent; branchlets sharply tetragonal. 7. *A. lanceolata*

m. Petiolar-scutum present; branchlets obscurely tetragonal n.

n. Branchlets and lower leaf-surfaces glabrous; petiolar-scutum conspicuous as a distinct sheath. 8. *A. sculigera*

n. Branchlets and lower leaf-surfaces thinly furfuraceous; petiolar-scutum wart-like. 9. *A. Pennellii*

k. Leaf-base neither cordate nor auriculate, often shortly decurrent, with the decurrent part sometimes expanded and recurved o.

o. Leaves 5-pli-nerved, sometimes only slightly so p.

p. Leaf-margins toothed, at least distally. 21. *A. Merianiae*

p. Leaf-margins entire q.

q. Leaves 15–30 cm. long. 11. *A. Drakei*

q. Leaves 6–14 cm. long r.

r. Petioles 1 cm. long; panicles few-flowered. 12. *A. pauciflora*

r. Petioles 2–4 cm. long; panicles many-flowered. 13. *A. speciosa*

o. Leaves 5–7-nerved s.

s. Petiolar-scutum present t.

t. Branchlets dark and conspicuously lustrous; leaf-base not at all decurrent. 15. *A. nitida*

t. Branchlets not dark and conspicuously lustrous; leaf-base usually shortly decurrent, with the decurrent part recurved or expanded and crisped. 18. *A. grandifolia*

s. Petiolar-scutum absent u.

u. Submarginal veins the 6th and 7th; leaves 7–12 cm. long. 19. *A. macrophylla*

u. Submarginal veins the 4th and 5th; leaves 4–5 cm. long. 20. *A. affinis*

TREATMENT OF THE SPECIES

1. AXINAEA SESSILIFOLIA Triana, Trans. Linn. Soc. Bot. **28**: 69. 1871.

Branchlets tetragonal, keeled on the angles, greatly swollen at the nodes, with stipules persistent or stipule-scars prominent, glabrous; leaves *sessile or very nearly so*, elliptical-oblong, 15–20 cm. long, 6–10 cm. wide, obtuse at the apex, cordate at the base, entire, 5–7-pli-nerved, conspicuously reticulate, glabrous above and beneath, membranaceous; panicles pendulous, widely branched; pedicels glabrous, 8–10 mm. long; hypanthium cyathiform, glabrous, 8 mm. wide; calyx-limb subtruncate; petals oblong, rounded or barely retuse, 13 mm. long; filaments 6 mm. long; anther-sacs long-attenuate, 10 mm. long; connectives with large prominent dorsal lobe against the anther-sacs, apiculate, 4 mm. long; style abruptly curved near the tip, 8–9 mm. long.

ECUADOR—Chimborazo: *Spruce 6174*, type collection (K).

A. sessilifolia is a tree about 12 m. tall. The petals are blood-red and the anthers yellow. This species can be readily distinguished from the others of the genus by its sessile (or very nearly so) leaves. It is perhaps most closely related to *A. crassinoda*.

2. AXINAEA CRASSINODA Triana, Trans. Linn. Soc. Bot. **28**: 69. 1871.

Branchlets more or less tetragonal, *greatly swollen at the nodes*, with stipules persistent or stipule-scars very prominent, densely to thinly hirsute-pubescent; petioles stout, densely scurfy to hirsute, 4–7 cm. long, without a scutum; leaves broadly ovate, 13–19 cm. long, 12–16 cm. wide, obtuse and rounded at the apex, *cordate at the base, conspicuously crenate-dentate*, 7–9-nerved, conspicuously reticulate beneath, glabrous above, scurfy on the nerves and veinlets beneath, subcoriaceous; panicles pendulous, with spreading branches, about 16 cm. long; pedicels furfuraceous, 4–10 mm. long; hypanthium broadly cyathiform, finely furfuraceous, 7 mm. wide; calyx-limb broadly 4-lobed to truncate; petals 4, obovate, retuse, 8–10 mm. long; stamens 8; filaments 3–4 mm. long; anther-sacs 5 mm. long; connectives conic, acuminate, 4 mm. long; style slightly curved, 9–12 mm. long.

PERU—Prov. of Chachapoyas: *Mathews 3213*, type (K); Playampampa: *Macbride 4873* (F).

A. crassinoda is the only species of the genus having tetramerous flowers. It is most closely related to *A. sessilifolia*.

3. AXINAEA GLANDULOSA Ruiz & Pav. Fl. Per. **4**: t. 412. 1802.

Chastenaea glandulosa (Ruiz & Pav.) Naud., Ann. Sci. Nat. III. **18**: 123, 124. 1852.

Branchlets obscurely tetragonal, slightly swollen at the nodes but with stipule-scars not prominent, furfuraceous near the tips; petioles robust, somewhat furfuraceous, 2–4 cm. long, *with a conspicuous scutum;* leaves ovate, 10–15 cm. long, 5–7 cm. wide, acute at the apex, *auriculate at the base, with the auricles reflexed*, entire or very minutely sinuate-denticulate, 5–7-nerved, glabrous above, *densely furfuraceous-tomentose beneath*, coriaceous; panicles erect, stoutly peduncled; pedicels thick, furfuraceous, 5–8 mm. long; hypanthium broadly campanulate, glabrous, rugose, 7 mm. wide; calyx-limb subtruncate; petals oblong-obovate, apiculate, 13 mm. long; filaments curved, 4–5 mm. long; anther-sacs 6 mm. long; connectives broadly ovate, flattened, obtuse or acute, 3 mm. long by 2½ mm. broad; style subfiliform, 15 mm. long.

PERU—Chinchao: *Ruiz s. n.*, type collection (B, K); near Pampayaca: *Kanehira 11* (F).

A. glandulosa has white flowers. The species is most closely related to *A. Weberbaueri*. It differs especially, however, in having obscurely tetrag-

onal and branchlets and the basal lobes of the leaf conspicuously reflexed. It is probably also related to *A. tomentosa*. The Ruiz collection from Chinchao and deposited at the Botanisches Museum has been considered by some to be the type collection of *A. lanceolata*. I am persuaded to agree with Markgraf, however, that the specimen represents *A. glandulosa*. It differs from *A. lanceolata* in having the leaves densely tomentose beneath, obscurely tetragonal branchlets, and a petiolar-scutum.

4. AXINAEA WEBERBAUERI Cogn., Engl. Bot. Jahrb. **50**: Beibl. III. 32. 1913.

Branchlets *acutely tetragonal*, slightly swollen at the nodes, furfuraceous-puberulent; petioles slender, furfuraceous, 1½–4 cm. long, with a small tubercle-like scutum; leaves narrowly ovate or ovate-lanceolate, 8–18 cm. long, 3–8 cm. wide, acuminate at the apex, obtuse or *generally small auriculate* at the base, minutely and remotely denticulate, 5-nerved, glabrous or sometimes furfuraceous-puberulent at the base above, *shortly and densely stellate-tomentose beneath*, coriaceous; panicles erect, densely many-flowered, about 5–8 cm. long; pedicels densely furfuraceous, 2–6 mm. long; hypanthium broadly campanulate, glabrous above, furfuraceous-puberulent at the base, 8 mm. wide; calyx-limb subtruncate; petals obovate to oblong, retuse, 10–16 mm. long; filaments 4½ mm. long; anther-sacs flattened, with two lateral wings running down from the connectives, 6 mm. long; connectives ovoid, acute or obtuse, 3 mm. long; style slender, sometimes abruptly curved at the top, 6–15 mm. long.

PERU—Prov. of Huanta: *Weberbauer 5648*, type (B), isotype (F).

A. Weberbaueri is a tree about 4 m. tall, occurring at an altitude of 2700–3000 m. The leaves are intensely green above and green to ashy beneath. The petals are violet or purple. This species is most closely related to *A. glandulosa*, from which it differs especially in having acutely tetragonal branchlets and the basal lobes of the leaf somewhat recurved but not conspicuously reflexed.

5. AXINAEA TOMENTOSA Cogn. DC. Monogr. Phan. **7**: 451. 1891.

Branchlets conspicuously tetragonal, slightly swollen at the nodes, with stipule-scars more or less obscure, furfuraceous; petioles stout, furfuraceous, 2–3½ cm. long, *with a scutum present* but sometimes much reduced; leaves broadly elliptical, 12–15 cm. long, 7½–8 cm. wide, apiculate to obtusely acuminate at the apex, acute and slightly revolute at the base, finely and remotely denticulate, 5–7-nerved, often slightly pli-nerved, glabrous above, *densely rusty-tomentose with plumose hairs beneath*, coriaceous; panicles erect, compact, many-flowered, about 9 cm. long; pedicels densely furfuraceous-puberulent, thick, 2–5 mm. long; hypanthium broadly campanulate, furfuraceous, *7–8 mm. wide;* calyx-limb truncate to shallowly 5-lobed; petals obovate to oblong, obtuse to subretuse, *12–15 mm. long;* filaments flattened-filiform, 6–8 mm. long;

anther-sacs 6–8 mm. long; connectives ovoid, with two large and somewhat flattened lateral lobes, blunt, 3 mm. long by 4 mm. broad; style slender, 17 mm. long.

PERU—Chachapoyas: *Mathews s. n.*, isotypes (Y, K, B); Prov. of Bongara: *Weberbauer 7150* (F, B).

A. tomentosa is a shrub about 4 m. tall, occurring at an altitude of 2500–2600 m. This species is most closely related to *A. sclerophylla*, from which it may be distinguished by the presence of a petiolar-scutum, a hypanthium 7–8 mm. wide, and petals usually less than 15 mm. long.

6. AXINAEA SCLEROPHYLLA Triana, Trans. Linn. Soc. Bot. **28:** 68. 1871.

Branchlets conspicuously tetragonal, swollen at the nodes, without stipule-scars, tomentose; petioles robust, tomentose, 2–3 cm. long, *without a scutum;* leaves broadly elliptical, 12–15 cm. long, 7–9 cm. wide, shortly and obliquely round-acuminate at the apex, with the acumen recurved, subacute at the base, with the basal margin slightly expanded and reflexed, remotely serrate on the upper half or entire, 5-pli-nerved, glabrous above, *densely rusty-tomentose with elongate plumose hairs beneath*, coriaceous; panicles axillary, few-flowered, cymose; pedicels stout, furfuraceous, 2–3 mm. long; hypanthium hemispheric, tomentose at the base, *12 mm. wide;* calyx-limb truncate; petals broadly obovate, retuse, *22 mm. long;* filaments 11 mm. long; anther-sacs subulate, 7–8 mm. long; connectives ovoid, somewhat flattened, blunt, 4 mm. long; style stout, curved at the top, 14 mm. long.

ECUADOR—region of Loja: *Seemann s.n.*, type (K).

A. sclerophylla is most closely related to *A. tomentosa*, and the two superficially resemble one another. The former, however, is characterized by petals commonly more than 20 mm. long, a hypanthium about 12 mm. wide, and the presence of a petiolar-scutum.

7. AXINAEA LANCEOLATA Ruiz & Pav. Fl. Per. **4:** t. 409. 1802.

Chastenaea lanceolata (Ruiz & Pav.) Naud., Ann. Sci. Nat. III. **18:** 123. 1852.

Branchlets *acutely tetragonal*, subglabrous; petioles slender, subglabrous, 5–6 cm. long, *without a scutum;* leaves ovate-lanceolate, 10–20 cm. long, 3–10 cm. wide, bluntly acuminate at the apex, auriculate at the base, *with the auricles conspicuously folded under*, remotely serrate, 5–7-nerved, glabrous above, subglabrous beneath, coriaceous; panicles pendulous, few-flowered, small; pedicels furfuraceous or glabrous, 5–10 mm. long; hypanthium broadly campanulate, granular-pubescent or glabrous, 6–11 mm. wide; calyx-limb subtruncate; petals oblong to obovate, rounded or retuse, 10–18 mm. long; filaments 3–5 mm. long; anther-sacs subulate, 5–8 mm. long; connectives ovoid, obtuse or acute, 3–4 mm. long; style filiform, 5 mm. long.

PERU—Sandillani: *Pearce s.n.* (K). BOLIVIA—Dept. of Cochabamba, Quebrada de Corani: *Steinbach 8861* (Y, B).

A. lanceolata is a shrub or tree up to 18 m. tall, occurring at an altitude of 2400–2700 m. The flowers range in color from pink to white, and blossom in June, July, and August. This species is perhaps most closely related to *A. scutigera*. From the material at hand it would seem that *A. lanceolata* and *A. scutigera* are too widely separated geographically to be very closely related. Nevertheless, these two species appear to be more closely related one to the other than to any of the other species of the genus.

8. AXINAEA SCUTIGERA Triana, Trans. Linn. Soc. Bot. **28**: 69. 1871.

Branchlets tegragonal, shining, glabrous; petioles slender, glabrous, 3 cm. long, *with a scutum conspicuous as a distinct sheath;* leaves ovate, 7–10 cm. long, 4–5 cm. wide, round-acuminate at the apex, *cordate at the base,* with the basal lobes sometimes reflexed, remotely sinuate-serrate, 7-nerved, conspicuously reticulate, glabrous above and beneath, coriaceous; panicles axillary, compact, irregularly branched; pedicels essentially glabrous, curved, 10 mm. long; hypanthium hemispheric, glabrous, 6 mm. wide; calyx-limb truncate; petals obovate, apiculate, 12–15 mm. long; filaments arcuate, 7 mm. long; anther-sacs subulate, 6 mm. long; connectives ovoid, flattened, blunt, 4 mm. long; style curved, 13 mm. long.

COLOMBIA—Prov. of Antioquia: *Triana s.n.*, type collection (K).

A. scutigera occurs at an altitude of 2500 m. This species is perhaps most closely related to *A. lanceolata*, which it somewhat resembles. It differs principally, however, by its conspicuously sheathing petiolar-scutum.

9. AXINAEA PENNELLII Gleason, Bull. Torr. Club. **54**: 28. 1927.

Branchlets *subterete,* becoming obscurely tetragonal near the tips, somewhat swollen at the nodes, *ochre-scurfy near the tips;* petioles slender, scarcely scurfy, 1½–2 cm. long, *with a minute wart-like scutum which is sometimes inconspicuous;* leaves long-ovate, 10–16 cm. long, 3½–6 cm. wide, blunt-acuminate at the apex, small auriculate at the base, *with the auricles reflexed and overlapping,* conspicuously sinuate-serrate, 5–7-nerved, glabrous above, thinly ochraceous-furfuraceous beneath, more or less coriaceous; panicles erect, about 10-flowered; pedicels thinly furfuraceous, 5–10 mm. long; hypanthium broadly hemispheric, glabrous or very thinly furfuraceous, 10 mm. wide; calyx-limb truncate; petals oblong-obcordate, retuse, 16 mm. long; filaments 7–10 mm. long; anther-sacs 6–9 mm. long; connectives ovoid, blunt, 5–6 mm. long; style 14 mm. long.

PERU—forested cliff above Rio Pillahaute: *Pennell 14003*, type (Y), cotype (F).

A. Pennellii is a tree occurring at an altitude of 2300–2400 m. The petals are purple. This species is probably most closely related to *A. lanceolata*, from which it is distinguished by its subterete or obscurely tetragonal branchlets and the presence of a petiolar-scutum.

10. AXINAEA DEPENDENS Ruiz & Pav. Fl. Per. **4**: t. 411. 1802.

Meriania dependens (Ruiz & Pav.) Naud., Ann. Sci. Nat. III. **18**: 124, 129. 1852.

Branchlets obscurely tetragonal, scarcely swollen at the nodes, *with stipules persistent and semi-circular*, finely furfuraceous, becoming glabrous; petiole slender to thickish, furfuraceous-puberulent, 1½–4½ cm. long, without a scutum; leaves elliptical-lanceolate, 11–16 cm. long, 3–5 cm. wide, acuminate at the apex, acute to rounded at the base, undulate-denticulate, *5-pli-nerved*, prominently reticulate beneath, glabrous above, furfuraceous-puberulent beneath, especially so along the nerves, submembranaceous; panicles pendulous, elongate, about 25 cm. long; pedicels puberulent, 10–12 mm. long; hypanthium hemispheric, finely furfuraceous, 5–7 mm. wide; calyx-limb obscurely 5-lobed; petals oblong-obovate, obtuse, 10–12 mm. long; filaments very flat, 5 mm. long; anther-sacs 6 mm. long; connectives narrowly conic, long acuminate, 5 mm. long; style attenuate, 12–18 mm. long.

PERU—Vitoc: *Ruiz s.n.*, type collection (B); Chichao: *Ruiz s.n.* (B), *Lobb s.n.* (K).

In *A. dependens* the leaves are intensely green above and ashy green beneath. It is probably most closely related to *A. lanceolata*, from which it is readily distinguished by the persistent and semi-circular stipules, the acute to rounded leaf-base, and the obscurely tetragonal branchlets. The specimen collected by Ruiz at Chinchao and now deposited at the Botanisches Museum, Berlin, has been considered by some to be the type collection of *A. glandulosa*. I am persuaded to agree with Markgraf, however, that this consideration is in error and that the particular specimen represents *A. dependens*. It differs from *A. glandulosa* in having pli-nerved leaves, persistent and semi-circular stipules, and no petiolar-scutum.

11. AXINAEA DRAKEI Cogn., DC. Monogr. Phan. **7**: 447. 1891.

Branchlets robust, somewhat furfuraceous-puberulent; petioles robust, somewhat furfuraceous-puberulent, 2–3 cm. long, without a scutum; leaves ovate-elliptical, *15–30 cm. long*, 8–15 cm. wide, obtuse at the apex, subrounded at the base, *entire*, *5-pli-nerved*, prominently reticulate beneath, glabrous above, furfuraceous-puberulent beneath, sometimes only so on the nerves, hardly coriaceous; panicles few-flowered, 10–15 cm. long; pedicels thick, short, very much flattened, minutely hirsute, 5–8 mm. long; hypanthium broadly campanulate, more or less furfuraceous-puberulent, 12–13 mm. wide; calyx-

limb subtruncate; petals obliquely obovate, 20 mm. long; filaments 7–8 mm. long; anther-sacs linear, 7–8 mm. long; connectives slightly thickened dorsally, acuminate; style thick, 12–13 mm. long.

ECUADOR—Quebrada near Loja: *Poortmann* in hb. Drakei. No specimens of this species were examined.

A. Drakei is a shrub 2–4 m. tall, with robust branches. The leaves are pallid above and dusky beneath. The petals are crimson. No specimens of this species were received from the herbaria from which sheets have been borrowed. The above description is based entirely upon Cogniaux's description as it occurs in DC. Monogr. Phan. **7**: 447, 1891. This species is probably most closely related to *A. pauciflora*, from which it is readily distinguished by the large leaves (15–30 cm. long). It may also be closely related to *A. speciosa*.

12. AXINAEA PAUCIFLORA Cogn., DC. Monogr. Phan. **7**: 448. 1891.

Branchlets rather slender, obtusely tetragonal, somewhat furfuraceous; petioles robust, more or less furfuraceous-puberulent, *1 cm. long*, without a scutum; leaves ovate, *6–9 cm. long*, 4–6 cm. wide, obtuse at the apex, subacute at the base, *entire*, *5-pli-nerved*, glabrous above, somewhat furfuraceous-puberulent beneath, scarcely coriaceous; panicles terminal, cymose, 5-flowered; pedicels somewhat slender, shortly hirsute, 10 mm. long; hypanthium broadly hemispheric, slightly furfuraceous-puberulent, 8–9 mm. wide; calyx-limb dilated, subentire; filaments 5 mm. long; anther-sacs linear, 5 mm. long; connectives narrowly ovoid, acute; style thick, 15 mm. long.

ECUADOR or PERU—*Grisar* in hb. Mus. Paris. No specimens of this species were examined.

In this species the leaves are pallid green above and ashy-green beneath with robust nerves. No specimens of this species occur among the herbaria sheets that have been borrowed. The description above is based entirely upon that of Cogniaux's in DC. Monogr. Phan. **7**: 448, 1891. *A. pauciflora* is probably most closely related to *A. Drakei*. The two may easily be distinguished by the length of the leaf: in the former the leaves are 6–9 cm. long, whereas in the latter they are 15–30 cm. long.

13. AXINAEA SPECIOSA Britt., Bull. Torr. Club **17**: 57. 1890.

Branchlets obscurely tetragonal, with stipule-scars not evident, slightly scurfy near the tips; petioles glabrous, 2–3½ cm. long, without a scutum; leaves lanceolate, 10–14 cm. long, 3–6½ cm. wide, obtuse at the apex, subrounded or acute at the base, *entire*, *5-pli-nerved*, conspicuously reticulate, glabrous above, slightly brown scurfy to glabrous beneath, coriaceous; panicles *densely flowered*, about 12 cm. long; pedicels slightly scurfy, 15 mm. long;

hypanthium broadly cyathiform, glabrous, 9 mm. wide; calyx-limb truncate to subtruncate; petals suborbicular, rounded, 15–24 mm. long; filaments 10 mm. long; anther-sacs attenuate, 10 mm. long; connectives conic, with a small prominent dorsal lobe, long acuminate; style filiform, slightly arcuate, 9–12 mm. long.

BOLIVIA—Mapiri: *Rusby 2328*, type (Y), isotypes (F, B); road from Pararani to Mapiri: *Tate 393* (Y) ; San Carlos: *Buchtien 1001* (B).

In *A. speciosa* the leaves are dark green above and pallid beneath. This species is probably most closely related to *A. Drakei* or *A. pauciflora*.

14. AXINAEA LEHMANNII Cogn., Engl. Bot. Jahrb. **8**: 20. 1886.

Branchlets obscurely tetragonal, somewhat swollen at the nodes, without stipule-scars or with stipule-scars scarcely evident, glabrous; petioles stout, glabrous, 1½–2 cm. long, with a minute scutum or sometimes without any; leaves ovate, 12–22 cm. long, 7–14 cm. wide, shortly round-apiculate at the apex, rounded and subemarginate-cordate at the base, *entire*, 7-nerved, infrequently pli-nerved, very prominently reticulate, *glabrous above and beneath*, coriaceous; panicles erect, moderate, pyramidal, many-flowered, about 10–12 cm. long; pedicels glabrous, 5–7 mm. long; hypanthium broadly cyathiform, glabrous, 8 mm. wide; calyx-limb truncate; petals obovate, retuse, 11–12 mm. long; filaments 6–8 mm. long; anther-sacs 10 mm. long; connectives ovoid, with a prominent dorsal and two prominent lateral lobes, acute or apiculate, 2–3 mm. long; style filiform, sharply bent over at the top, 10–18 mm. long.

COLOMBIA— *Lehmann BT. 997* (Y, K).

This species is a densely branched tree, about 5. m. tall. The branches become slender and lightly arcuate. The leaves are widespread, an intense shining green above and pallid beneath. The nerves are stong and deeply impressed above. The flowers have reddish petals. *A. Lehmannii* is perhaps most closely related to *A. grandifolia*, but the leaves are 7-nerved and entire, not 5-nerved and with margins sinuate-dentate.

15. AXINAEA NITIDA Cogn., Engl. Bot. Jahrb. **42**: 138. 1906.

Branchlets obscurely tetragonal, furfuraceous-puberulent, becoming glabrous, *dark and conspicuously lustrous;* petioles slender, furfuraceous or glabrous, 1–4 cm. long, *with a tubercle-like scutum;* leaves narrowly ovate, 5–9 cm. long, 3½–5 cm. wide, short-acuminate at the apex, *rounded at the base*, undulate-denticulate, especially distally, sometimes nearly entire, 5-nerved, *with the reticulation elevated beneath*, glabrous and *lustrous* above, somewhat furfuraceous or glabrous beneath, coriaceous; panicles short, densely and many-flowered, about 6 cm. long; pedicels glabrous to slightly furfuraceous, 3–8 mm. long; hypanthium hemispheric, glabrous, 6–7 mm. wide; calyx-limb truncate to shallowly undulate; petals obovate, rounded to very slightly

retuse, 10–14 mm. long; filaments 6 mm. long; anther-sacs 5 mm. long; connectives ellipsoidal, blunt, 4 mm. long; style subfiliform, 11–15 mm. long.

PERU—Dept. of Amazonas, Molinipampa: *Weberbauer 4355*, type (B); *Mathews 1287* (K).

A. nitida is a shrub about 2 m. tall, with robust branches and dark lustrous branchlets. The flowers bloom in July, and have reddish petals. This species is similar to *A. grandifolia*. *A. nitida*, however, may be readily distinguished by its lustrous branchlets and upper leaf-surfaces, and its never decurrent leaf-bases.

16. **Axinaea robusta** D. Eves, sp. nov.

Ramuli robusti, manifeste tetragoni, ad nodos valde incrassati, cicatricibus stipularum manifeste incrassatis, furfuracei, demum glabri; petioli robusti, 2–4 cm. longi, furfuracei, scuto conspicuo; laminae ovato-lanceolatae, 9–16 cm. longae, 5–10 cm. latae, apice acuminatae, basi subrotundatae et parum auriculatae, auriculis nonnihil recurvis, valde minute sinuato-denticulatae vel subintegrae, 5–7-nerviae, supra glabratae, subtus praecipue ad venas venalasque furfuraceae, subcoriaceae; paniculae pendulae, robuste pedunculatae, 15 vel plus cm. longae; pedicelli graciles furfuracei, 10 mm. longi; hypanthium semiglobosum, glabrum, 7 mm. latum; limbus calycis subtruncatus; petala suborbicularia, rotundata, 9 mm. longa; filamenta 4 mm. longa; thecae 6 mm. longae, connectivis ovoideis, planis, apiculatis, 4 mm. longis; stylus robustus, 7 mm. longus.

Branchlets robust, *conspicuously tetragonal, greatly swollen at the nodes, with stipule-scars prominently thickened*, furfuraceous, becoming glabrous; petioles robust, furfuraceous, 2–4 cm. long, with a conspicuous scutum; leaves ovate-lanceolate, 9–16 cm. long, 5–10 cm. wide, acuminate at the apex, *subrounded and small auriculate at the base*, with the auricles somewhat recurved, very minutely sinuate-denticulate or almost entire, 5–7-nerved, glabrous above, furfuraceous beneath especially along the nerves and veins, subcoriaceous; panicles pendulous, stoutly peduncled, 15 or more cm. long; pedicels slender, furfuraceous, 10 mm. long; hypanthium hemispheric, glabrous, 7 mm. wide; calyx-limb subtruncate; petals suborbicular, rounded, 9 mm. long; filaments 4 mm. long; anther-sacs 6 mm. long; connectives ovoid, flattened, apiculate, 4 mm. long; style stout, 8 mm. long.

COLOMBIA—Mont del Moro: *Purdie s.n.*, type (K).

Purdie records that he has observed panicles of this species 2–3 feet long. The small auriculate leaf-base is very significant, appearing much as if the auricles are expanded and somewhat recurved decurrent portions of the leaf blade. *A. robusta* is perhaps most closely related to *A. grandifolia*, differing from it principally by the conspicuously tetragonal branchlets greatly swollen at the nodes.

17. AXINAEA COSTARICENSIS Cogn., DC. Monogr. Phan. **7**: 1182. 1891.

Branchlets obscurely tetragonal, scarcely swollen at the nodes, *with stipule-scars very prominent as thickened rings*, furfuraceous, becoming glabrous; petioles slender, glabrous to slightly furfuraceous, 2–4 cm. long, *with a tubercle-like scutum well below the blade and connected with it by narrow lateral recurved wings;* leaves ovate, 9–18 cm. long, 5–8 cm. wide, obtuse at the apex, narrowed and subrounded at the base, entire or minutely and remotely denticulate, 5–7-nerved, glabrous above, glabrous to slightly furfuraceous beneath, submembranaceous; panicles erect or subpendulous, broadly pyramidal, many-flowered, about 20 cm. long; pedicels furfuraceous, 5–10 mm. long; hypanthium hemispheric, essentially glabrous, 7 mm. wide; calyx-limb subtruncate; petals obovate, retuse, 10–15 mm. long; filaments 3 mm. long; anther-sacs 3 mm. long; connectives ovoid, apiculate in the rear, 3 mm. long; style 5–10 mm. long.

COSTA RICA—Isla del Rio Mancaron: *Pittier 2007*, type (B), isotype (F); Varablanca, Sarapigui: *Werckle 16687* (F).

A. costaricensis occurs at an altitude of about 2100 m. It is the only species of *Axinaea* that has as yet been found outside of South America. This species is probably most nearly related to *A. grandifolia*.

18. AXINAEA GRANDIFOLIA (Naud.) Triana, Trans. Linn. Soc. Bot. **28**: 69. 1871.

Chastenaea grandifolia Naud., Ann. Sci. Nat. III. **18**: 122. 1852.

Branchlets obtusely tetragonal, pulverulent near the tips, becoming glabrous; petioles slender, pulverulent, 3–4 cm. long, *with a transverse tubercled scutum;* leaves narrowly ovate, 7–16 cm. long, 6–7 cm. wide, shortly round-apiculate at the apex, rounded and *generally shortly decurrent* at the base, in the latter case the lower extremity of the decurrent portion recurved or expanded and crisped, sinuate-dentate, 5–7-nerved, more or less conspicuously reticulate, glabrous above, glabrous to somewhat furfuraceous beneath, coriaceous; panicles erect, many-flowered, subcorymbose; pedicels pulverulent, 8–12 mm. long; hypanthium broadly hemispheric, glabrous or essentially so, 7–8 mm. wide; calyx-limb subentire; petals broadly obovate, retuse to apiculate, 10–12 mm. long; filaments 2 mm. long; anther-sacs flattened, 5 mm. long; connectives ovoid to rotund, apiculate to blunt, 2 mm. long; style robust to subfiliform, slightly arcuate, 7–8 mm. long.

VENEZUELA—Prov. of Merida: *Moritz 959*, cited by Cogn. (B, K), *Funck and Schlim 1253*, cited by Cogn. (G). COLOMBIA—Dept of Santander: *Kalbreyer 749* (B, K). PERU—Huanuco, Pan de Azucar: *Sawada 68* (F).

A. grandifolia has purple-petaled flowers. This species is somewhat variable. It is probably most closely related to *A. macrophylla*, which it

more or less resembles. *A. grandifolia*, however, has a petiolar-scutum and flowers distinctly smaller and more numerous.

19. AXINAEA MACROPHYLLA (Naud.) Triana, Trans. Linn. Soc. Bot. **28**: 69. 1871.

Chastenaea macrophylla Naud., Ann. Sci. Nat. III. **18**: 121. 1852.
Chastenaea floribunda Naud., Ann Sci. Nat. III. **18**: 122. 1852.
Axinaea floribunda (Naud.) Triana, Trans. Linn. Soc. Bot. **28**: 69. 1871.

Branchlets obscurely tetragonal, glabrous to densely brown-pulverulent; petioles slender, glabrous or furfuraceous, 2–4 cm. long, *without a scutum;* leaves elliptical, 7–12 cm. long, 2–5 cm. wide, acute or shortly round-apiculate at the apex, *rounded or somewhat attenuate with recurved margins at the base,* sinuate-serrate at least distally or almost entire, *7-nerved,* glabrous above, glabrous or furfuraceous beneath, coriaceous; panicles pendulous, compact, cymose, short; pedicels furfuraceous, 5–10 mm. long; hypanthium hemispheric, glabrous or scarcely furfuraceous, 6–8 mm. wide; calyx-limb truncate or distinctly 5-sinuate; petals obovate, retuse, 8–12 mm. long; filaments 4–6 mm. long; anther-sacs 5–7 mm. long; connectives broad, flattened, obtuse or acute, 3–5 mm. long; style 8–15 mm. long.

COLOMBIA—Bogota: *Woronow & Juzupczuk 5084* (Y), *Triana s.n.* (Y, K), *Holton 907* (Y, K), *Tracey 299* (K); Dept. of El Cauca: *Pennell & Killip 6506* (Y, B), *Pennell 7112* (Y), *Killip 6798* (Y); Quindio: *Triana s.n.* (Y); *Bro. Ariste-Joseph B-14* (Y); *Triana 5832* (Y, K); *Jameson 451* (K, G); Central Andes of Popayan: *Blakes 8649* (K); Eastern Paramos of Guasca: *Bro. Ariste-Joseph s.n.* (F); Antioquia: *Lehmann 7446* (B), *Pennell 4259* (Y); Dept. of Santander: *Killip & Smith 17824* (Y, F), *Killip & Smith 17834* (Y); Dept. of Caldas: *Killip & Hazen 9474* (Y); *Linden 768* (F, K); *Lehmann 8649* (Y). ECUADOR—Prov. of Azuay and Canar, between Cuenca and Huigra: *Hitchcock 21677* (Y); Prov. of Loja: *Hitchcock 21436* (Y); *Spruce 5831* (K, B); *Lehmann 4653* (B); *White 4/72* (K).

A. macrophylla is a shrub or tree occurring at an altitude of 1800–3300 m. The petals are pale-pink to deep-pink, sometimes white. The flowers blossom in October and November. This species is perhaps most closely related to *A. grandifolia*, from which it differs principally in the absence of a petiolar-scutum. *A. macrophylla* bears some resemblance to *A. affinis*. In the former, however, the submarginal nerves are the 6th and 7th, whereas in the latter they are the 4th and 5th.

Formerly, *A. macrophylla* and *A. floribunda* were considered as separate species. Comparison of a large number of herbarium specimens, however, shows that the one grades imperceptibly into the other. Accordingly, I have here combined the two groups into the one species: *A. macrophylla*.

The "Index Kewensis" lists *Chastenaea affinis* Naud. as a synonym for *A. macrophylla*. Cogniaux, however, (DC. Monogr. Phan. **7:** 1891) records *C. affinis* as a synonym for *Axinaea affinis* Cogn. In the present paper Cogniaux's synonymy is looked upon as the correct one and is, accordingly, herein adopted.

20. AXINAEA AFFINIS (Naud.) Cogn., DC. Monogr. Phan. **7:** 449. 1891.

Chastenaea affinis Naud., Ann. Sci. Nat. III. **18:** 120. 1852.
Axinaea macrophylla (Naud.) Triana, pro parte, Trans. Linn. Soc. Bot. **28:** 69. 1871.

Branchlets obscurely tetragonal, glabrous; petioles slender, glabrous, 1–2 cm. long, without a scutum; leaves ovate, *4–5 cm. long*, 2–3 cm. wide, obtuse at the apex, acute and shortly revolute-decurrent at the base, remotely sinuate-serrate, especially so distally, *5-nerved, with the secondaries conspicuous and brown*, prominently reticulate, glabrous above, very thinly furfuraceous beneath or glabrous, coriaceous; panicles pendulous, cymose, few flowered; pedicels essentially glabrous, 10 mm. long; hypanthium hemispheric, essentially glabrous, 7 mm. wide; calyx-limb truncate; petals obovate, retuse, 12–15 mm. long; filaments 6–8 mm. long; anther-sacs 6 mm. long; connectives ovoid, with a prominent dorsal lobe, acuminate; style thickish, 15–20 mm. long.

COLOMBIA—Prov. of Ocana: *Schlim 304*, cited by Cogn. (K). ECUADOR—between Sarajuro and San Lucas: *Jameson 143* (K); San Lucas: *Jameson s.n.* (F).

A. affinis occurs at an altitude of 3300–3700 m. The leaves are intensely green above and pale beneath. The petals are purple. This species is somewhat similar to *A. Merianiae* and *A. macrophylla*. It differs, however, from the first in having leaves not at all pli-nerved and a hemispheric hypanthium, and from the second in having leaves 4–5 cm. long with the submarginal nerves the 4th and 5th. *A. affinis* is probably most closely related to *A. macrophylla*. The synomymy listed above is taken from Cogniaux (DC. Monogr. Phan. **7:** 449. 1891).

21. AXINAEA MERIANIAE (DC.) Triana, Trans. Linn. Soc. Bot. **28:** 69. 1871.

Chastenaea Merianiae DC. Prodr. III. 102. 1828.

Branchlets obscurely tetragonal, becoming terete, glabrous; petioles slender, glabrous, 1½–2 cm. long, without a scutum; leaves elliptical, 4–6 cm. long, 2½–3 cm. wide, acute or obtuse at the apex, acute to narrowed and shortly revolute-decurrent at the base, with the decurrent portion sometimes conspicuously expanded and reflexed, sinuate-serrate, *3–5-pli-nerved*, glabrous above and beneath, subcoriaceous; panicles subnutant, somewhat corymbose,

few-flowered, short; pedicels glabrous, 10 mm. long; *hypanthium shallowly saucer-shaped or broadly campanulate and depressed*, glabrous, 7–10 mm. wide; calyx-limb dilated, often reflexed, truncate to shallowly 5-sinuate; petals obovate, retuse, 12–15 mm. long; filaments 3–5 mm. long; anther-sacs 4 mm. long; connectives ovoid to rotund, large, blunt, 3–4 mm. long; style attenuate, 9–15 mm. long.

ECUADOR—Tambo de Cotosacapi: *Seemann 770*, cited by Cogn. (K); Azogues: *Lehmann 8533* (B). PERU—Dept. of Piura, prov. of Ayavaca: *Weberbauer 6371* (F, Y, B); Dept. of Libertad, prov. of Otuzco: *Weberbauer 6997* (B).

A. Merianiae is a shrub up to 5 m. tall, occurring at an altitude of 2900 m. The flower has a white to rose-colored corolla, and stamens with white filaments, yellow anthers, and dark red-violet connectives. This species is probably most closely related to *A. affinis*, which it often somewhat resembles. *A. Merianiae*, however, has leaves 3–5-pli-nerved, a depressed hypanthium, and large more or less ellipsoidal connectives which are blunt in the rear. *A. affinis*, on the other hand, has 5-nerved leaves (not at all pli-nerved), a broadly hemispheric hypanthium, and ovoid connectives which are acuminate in the rear.

22. AXINAEA LEPIDOTA (Benth.)Triana, Trans. Linn. Soc. Bot. **28:** 69. 1871.

Chastenaea lepidota Benth., Pl. Hartw. 182. 1845.
Chastenaea coriacea Naud., Ann. Sci. Nat. III. **4:** 55. 1845.

Branchlets more or less tetragonal, *whitish-arachnoid on the younger parts;* petioles slender, whitish-arachnoid when young, 8–12 mm. long, without a scutum; leaves elliptical, *3–5 cm. long*, 1–2 cm. wide, obtuse at the apex, rounded and sometimes slightly revolute-decurrent at the base, entire or minutely and remotely sinuate on the upper half, 3–5-pli-nerved, sometimes only scarcely pli-nerved, glabrous above, *whitish-arachnoid beneath* especially when young, coriaceous; panicles erect, cymose, few-flowered, short; pedicels whitish-arachnoid to scarcely so, 5–10 mm. long; hypanthium hemispheric, glabrous or scarcely whitish-arachnoid at the base, 10–11 mm. wide; calyx-limb subtruncate; petals obovate, strongly asymmetrical, apiculate, 14 mm. long; stamens often stunted or imperfectly developed; filaments 7–8 mm. long; anther-sacs attenuate, normally 9 or more mm. long; connectives ovoid, acute or apiculate, 2 mm. long; style sometimes slightly arcuate, 10–12 mm. long.

ECUADOR—Province of Cuenca: *Hartweg 1014*, type (K), isotypes (B, G), *Lehmann 4924* (F, B), *Jameson 15* (K); Prov. of Loja: *Rose 23116* (Y), *Hitchcock 21573* (Y); Tipococha: *Diels 546* (B); Nabon: *Rose 22992* (Y); *Jameson s.n.* (F).

A. lepidota is a shrub up to 2–3 m. tall, occurring at an altitude of 2900–3300 m. The leaves are shining green above, becoming nigrescent when dry. This species is characterized, at least when young, by a whitish arachnoid pubescence. It is probably most closely related to *A. affinis* or *A. Merianiae*. It differs from these, however, in having smaller leaves (commonly less than 5 cm. long) and the whitish-arachnoid pubescence.

DOUBTFUL SPECIES

Axinaea quitensis R. Benoist, Bull. Soc. Bot. France **81**: 326. 1934.

Because the type is not available and because the description is not distinctive enough, I am unable to definitely consider this species. It is not possible, I believe, from the description of the species to distinguish between it and *A. macrophylla* Triana. Benoist asserts that *A. quitensis* differs from *A. macrophylla* by its glabrous condition, its clearly lobed calyx-limb, and its much smaller leaves (6–8 cm. long). Upon an examination of a large number of *A. macrophylla* specimens, however, these distinctions do not, in my opinion, appear to hold.

ECUADOR—Paramo de San Juan: *Benoist 3941*, type (Paris), not available.

EXCLUDED SPECIES

Axinaea tetragona Cogn., Engl. Bot. Jahrb. **42**: 137. 1908.

This species is excluded because it does not have the characteristic *Axinaea* stamen. The connectives are scarcely inflated and have two spurs, one projecting from the rear and another ascending parallel to the anther-sacs. The structure is that of *Meriania*. The species appears to be most closely related to *M. radula* Triana, differing mainly in having the leaves smooth above instead of rough. I have not, however, examined any specimens of *M. radula* for comparison.

PERU—Dept. of Amazonas, between Tambo Almirante and Tambo Bagazan: *Weberbauer 4430* (B), labeled as the type specimen of *Axinaea tetragona* Cogn.

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1931–1935

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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